SYSTEMATIC MAMMALOGY

CONTRIBUTIONS IN HONOR OF GUY G. MUSSER

EDITED BY

ROBERT S. VOSS AND MICHAEL D. CARLETON

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

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JOHN H. WAHLERT

PREFACE

Cut in stone over the entrance to the Ruthven Museum at the University of Michigan are the words "Go to nature, take the facts into your own hands; look, and see for yourself." Like many other museum graduate students, I came to regard those words (attributed to Louis Agassiz) as the essence of what we were being taught to do. Later, I came to appreciate how well they described Guy's research.

Guy was still a huge presence at Michigan, although he had not been there in person for 10 years, when I arrived in 1976. His specimens (impeccably prepared) filled dozens of drawers in the collection, his field notes (inimitably written) occupied several inches of shelf space in Hooper's office, and his publications (incomparably illustrated) already took up most of a file drawer in the Mammal Division library. His was an inspiring but daunting example for a neophyte researcher.

Guy's career began just as the influence of the New Systematics was beginning to wane. An earlier generation of mammalogists, encouraged by population geneticists to interpret taxonomic differences as geographic variation, had indulged in an orgy of lumping, synonymizing hundreds of valid taxa into undiagnosable polytypic "species," often without even a token analysis of relevant data. The most egregious lumping was perpetrated by authors of continentwide checklists, notably Ellerman and Morrison-Scott (in Eurasia) and Angel Cabrera (in South America). Much of the progress in late 20th-century mammalian systematics consisted in rediscovering the diversity of species then concealed by synonymy, and in providing the diagnostic tools—new characters and ways of analyzing them—by which that diversity could be documented.

More than any other mammalogist of his generation, Guy showed that comparative morphology was largely adequate to this task. All you had to do was look at the specimens (take the facts into your own hands), be able to see what you were looking at, and have the mother wit to draw the right conclusions. Most of us are influenced, to some extent at least, by what others have written or said about a long-standing research problem. One of Guy's great gifts, I think, is to be undeceived by the opinions of others and to focus on the facts. He also documented those facts (patterns of morphological character variation) and explained their taxonomic interpretation with exceptional clarity. His publications set new standards in systematic mammalogy.

In organizing Guy's festscrift, Mike and I decided that it would be more fitting to have just a few substantive contributions than to have a larger number of shorter papers. As it turned out, a "few" substantive contributions was plenty, as the heft of this volume attests. Among the many people who deserve our thanks for helping make this project a reality, we are particularly grateful to Nancy Simmons (who husbanded the Taxonomic Mammalogy funds to pay for most of it), to the late Karl Koopman (who endowed the Taxonomic Mammalogy Fund), to Mary Knight (who midwifed the manuscript through the production process), and to our many colleagues who reviewed manuscripts of individual chapters (acknowledged by name, unless anonymous, therein). Supplementary funds that helped defray publication costs were generously provided by the City College of New York, by the Division of Mammals at the Field Museum, and by the Department of Vertebrate Zoology and the Office of Research and Collections at the National Museum of Natural History.

Robert S. Voss
October 16, 2009

Chapter 1

They Sort Out Like Nuts and Bolts: A Scientific Biography of Guy G. Musser

MICHAEL D. CARLETON[1]

INTRODUCTION

"They sort out like nuts and bolts," or similar wording, was an assertion that regularly arose in my conversations or correspondence with Guy over the past 40 years. The "they" in this statement are species of Indo-Australian rodents (Muroidea: Muridae: Murinae), a diverse and taxonomically complex Old World group that would dominate his research contributions and secure his professional reputation as one of the foremost systematic mammalogists of his generation. The statement carried an implicit comparative context: it referenced Guy's formative experiences with a comparably complex group of New World rodents, deer mice of the genus *Peromyscus* (Muroidea: Cricetidae: Neotominae), research that comprised some of his earliest taxonomic works. The subtle features consulted to distinguish *Peromyscus* species served to sharpen his eye for specific discrimination whenever applied to other muroid genera investigated thereafter, particularly *Rattus* and kin.

> There is so much that needs to be done, so many groups [of Indo-Australian murids] that require good systematic revision, and just not enough time. *Melomys* is another example of a bottomless pit... All the previous work on the genus has been terrible.[2] We would not have had this problem if everyone had first worked and honed their skills on *Peromyscus*. (GGM, in litt., 31 March 1987)

How this innate, finely calibrated sense of discrimination as perfected through experiences with New World cricetids would lead to sorting the nuts and bolts of Old World murines is a story that bears telling from the beginning, at least from the academic beginnings.

ACADEMIC AND MUSEUM FOUNDATIONS (1956–1966)

> Inevitabilities of a life lived are a beginning and an end. (GGM, in litt., 23 September 1997, apropos the sudden death of Karl Koopman, longtime friend and colleague in the American Museum of Natural History)

Guy Graham Musser was born 10 August 1936 in Salt Lake City, Utah, and there attended elementary and secondary public schools until 1955. Like many of his contemporaries who entered the profession of mammalogy in the middle 1900s (e.g., see various autobiographies in Phillips and Jones, 2005), Guy recalls a boyhood compulsion to be outdoors and a preference for activities that indulged his enjoyment of the natural world. The family lived on the outskirts of Salt Lake City, from where he liked to take a bus, east to the foothills of the Wasatch Mountains or west to the Great Salt Lake Desert, hike around all day, and catch a returning bus in the evening. Other foothills nearer home harbored a cool mountain stream and the site of his earliest attempts at trout fishing, which was to become a lifelong pursuit, partly escapist recreation and partly ongoing education. He and friends

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[2] Not long afterward, rigorous taxonomic reviews of the genus appeared (Menzies, 1990, 1996).

used to scout *Microtus* runways and occasionally hand-capture a slow-footed vole that they would observe in an old washtub outfitted as a makeshift terrarium. Membership in the Boy Scouts afforded more opportunities for exploring different landscapes around Salt Lake City, including annual weeklong hikes into the Uinta Mountains, where he first experienced untrammeled wilderness away from human sign. Although undirected and diffusely experienced, such snatches of earliest memories presaged a deep attraction to and comfort with the outdoors.

Guy entered the University of Utah in the fall of 1955, having no predetermined field of matriculation, but his unabating curiosity about all things natural and a preference for being outdoors attracted him to a major in biology by his sophomore year. The university offered broad training in natural history and field biology, with many "-ology" courses—entomology and aquatic entomology, limnology, ichthyology, ornithology, mammalogy—that are no longer commonplace in today's university curricula, even in universities with natural history museums (e.g., see Schmidly, 2005). Guy thrived in such courses and happily immersed himself in counting diatoms to assay water quality, learning fish anatomy to identify native minnows, or keying out dragonflies by the patterns of wing venation. The classes satisfied his inclination to gain a hands-on understanding of natural systems, while actually requiring field trips, specimen collection, and species identification as part of the coursework. Furthermore, they planted the idea that diversionary pastimes enjoyed aimlessly as a youngster might be pursued as an equally rewarding and legitimate vocation as an adult. While still an undergraduate, extracurricular work connected with his aquatic entomology class fortuitously led to participation in major collecting expeditions along the Colorado River (Glen Canyon) and Green River (Flaming Gorge), undertaken in anticipation of impoundments planned along the upper Colorado drainage. Angus M. Woodbury and Stephen D. Durrant, respectively an entomologist and mammalogist in the university's Department of Zoology and Entomology, coordinated these field surveys, and Guy's responsibilities involved the collecting of aquatic insects and limnological data, not mammals. His first scientific article (1)[3], published in 1960 with aquatic entomologist G.F. Edmunds, documented the mayfly fauna gathered along the Green River.

Guy took Durrant's mammalogy course in his senior year. Durrant's class emphasized practical aspects of field mammalogy and required that the students set traplines, prepare study skins (his first a *Peromyscus maniculatus*!), and identify specimens. Again, his boyhood experiences—hiking around different habitats and chasing rodents—served him well in the mammalogy course: trapping mammals seemed to come as if second nature. Perhaps the inherent mystery kindled by the setting of a trap and attendant curiosity over what small mammal might appear in the next day's catch helped to shift his interest from insects to mammals. Equally or more pivotal were his interactions with M. Raymond Lee, a senior doctoral student of Durrant. Lee helped Guy with the identification of any unknowns captured in his traplines, discussed where to find and how to trap certain mammals, and shared the results of his own thesis research. By the close of the mammalogy course and after further consultation with Lee, Guy had decided to pursue systematic mammalogy and approached Durrant to accept him as a graduate student. After completing a bachelor of science degree in 1959, Guy thus remained at the University of Utah for postgraduate study (1959–1961). The composition and synergy of one's graduate student cohort play an important role in our higher education, perhaps as influential as courses taken, favorite professors, and committee chairs. In both stages of Guy's graduate study, first at the University of Utah (Ray Lee, Gary Ranck) and later at the University of Michigan (Jim Brown, Dave Klingener, Tim Lawlor), he enjoyed interactions with individuals who would become

[3] To avoid duplication, numbers in parentheses correspond to Musser's publications as enumerated chronologically and consecutively in appendix 1. Non-Musser citations are found in References.

dedicated and respected mammalogists in their own careers.

Guy's master's thesis entailed months of basic field survey, during which he honed his knowledge of where mammals lived and which traps and methods performed best to catch them. It also required much attendant curation in the department's expanding Museum of Zoology, processing and identifying his collections. The resulting faunal study on the "Mammals of the Tushar Mountains and Pavant Range in southwestern Utah" (M.S., 1961) was never published as such, but specimens from this fieldwork contributed to Guy's first papers on mammals, which involved new records of bat distribution (2) and description of a new subspecies of flying squirrel (3). Range extensions and subspecies descriptions were customary and respectable teething studies for a young systematic mammalogist coming of age during the middle 1900s.

Durrant had earned his doctorate at the University of Kansas (KU; Ph.D., 1950), under the direction of the preeminent mammalogist E. Raymond Hall. The Utah-Kansas academic connection offered a logical career path, for example, as was followed by Henry W. Setzer, one of Durrant's earlier master's students who relocated to KU to complete a doctoral thesis under Hall. Or, as encouraged by Durrant, Guy could stay at Utah and there continue a Ph.D. dissertation. He was uninterested, however, in conducting another "mammals of" faunal study, such as that undertaken for his M.S. degree. At some point during his master's study, Lee had enthusiastically shown him a paper by Emmet T. Hooper on the phallic anatomy of *Peromyscus* (Hooper, 1958). That study, along with Hooper's (1952) revision of Central American *Reithrodontomys*, indelibly impressed Guy for their thoroughness, taxonomic scope, and novel evolutionary insights. Hooper, together with William H. Burt, was a curator in the Museum of Zoology, University of Michigan (UMMZ), and the two were there developing a first-class graduate program in systematic mammalogy. Like Hall, Hooper and Burt were the academic progeny of Joseph Grinnell, curator and professor in the prestigious Museum of Vertebrate Zoology, University of California, and both were devoted adherents to field-oriented, museum-based systematic research as inspired by the model of their major professor. Although remaining at Utah to study under Durrant was the comfortable choice, the prospects of a new university environment and different research challenges persuaded Guy to write Hooper and ask about possibilities of graduate study at the UMMZ. Following a summer spent collecting birds throughout Utah for William H. Behle, his ornithology professor at Utah, Guy drove his '59 Chevy pickup cross-country to the flat upper Midwest and entered the University of Michigan in the fall of 1961.

The move to the University of Michigan conferred an ideal wedding of the field-collecting enthusiasm of a young graduate student, pursued in the setting of a major university-based natural history museum, under the tutelage of a critically minded systematist. After a year of earning his keep as a teaching fellow, Guy served as research assistant to Hooper, initiating the research that led to their minor classics on *Peromyscus* classification and muroid interrelationships (4, 5). In 1962, Guy and fellow grad student Dave Klingener accompanied Hooper for fieldwork in Costa Rica. Here, Guy first experienced trapping in tropical forests, lowland and montane, and was introduced to a rodent fauna very different from that of the Intermountain West. At Michigan, Guy's field talents were legendary to the grad students of my generation. The symmetry and natural proportions of a Musser study skin are readily identifiable within a drawer of rats and were emulated as the embodiment of a properly prepared round skin. Even so reserved a person as Hooper frankly regarded Guy as the best field person with whom he had ever associated, and Durrant grudgingly acknowledged (fide Hooper) the superior trapping abilities of "that damned hippie" (well, it was the '60s).

Guy's doctoral thesis (Ph.D., 1967) involved systematic study of a tree squirrel of northern Middle America: "A systematic study of the Mexican and Guatemalan gray squirrel *Sciurus aureogaster*, F. Cuvier (Rodentia, Sciuridae)." Many taxa now associated with this species—such as *griseoflavus*,

nelsoni, *poliopus*, and *socialis*—were formerly viewed as an intractable species complex whose populations exhibit exceptional variation in pelage color and pattern. Hooper had been intrigued by the problem, stimulated by his own Mexican fieldwork and specimen examination, and its resolution required the assembly of more material from regions undocumented by museum specimens, as well as the synthesis of extant museum holdings. Such needs suited his student's desire to return regularly to the field and see new environments, which Guy did in stints of 3–4 months over the years 1963–1965. The basic questions posed (Musser, 1968 [9]: 6) were "how many gene pools" are represented by *aureogaster* and related forms and "what are the morphological and ecological characteristics of these pools"? Pelage patterns of the nape, rump, and venter were meticulously quantified and collated geographically to infer intergradation among named forms and directions of gene flow; he concluded that the several names represent interbreeding populations of one immensely variable species, *S. aureogaster*, with only two broadly defined subspecies. The invocation of gene pools, directions of gene flow, and genetic isolation, as inferred from sample frequencies of chromatic traits, may sound anomalous when juxtaposed against gene sequencing, today's taxonomic tool of choice for understanding such population-level processes. Nevertheless, the terminology echoes the vocabulary and population thinking of the New Systematics and Evolutionary Synthesis, wherein the circumscription of definable geographic races (subspecies) presumably reflected underlying patterns of genetic discontinuity among populations and the potential evolution of nascent species. His dissertation represents a fine example of the subspeciation studies that unfolded in mid-century (e.g., Setzer, 1949; Hoffmeister, 1951; Anderson, 1956; Bowen, 1968).

Curiously, Guy's thesis on *Sciurus aureogaster* (9), with its emphases on intraspecific variation and infraspecific taxa, is atypical of the subsequent research that would characterize his prolific contributions on murine rodents of Asia and Indo-Australia. Instead, the reports on his field collections of *Peromyscus* made while at the UMMZ (6, 10) and collaborations with Hooper on muroid phallic morphology (4, 5) better preview his future research methodology and its emphasis on taxonomic ranks at the species level and above. The interactions with and standards set by Hooper while at Michigan, whether in the curation of collections or the conduct of systematic research, proved transformative. He afterward acknowledged Hooper's professional example on many occasions and in different contexts, for instance, apropos the tedious review of a long, meandering paper:

> It is not the kind of report Hooper would have allowed to see the light of day—either I am getting older and more mellow or I am just appreciating what I learned from him. I realize now that he allowed you to express your imagination and use innovation in preparing results but also insisted on rigorous documentation and clear presentation. (GGM, in litt., 31 March 1988)

Rigorous documentation and clear presentation would become hallmarks of his systematic contributions throughout the next phase of his career in the Department of Mammalogy at the American Museum of Natural History (AMNH).

The circumstances that brought Guy to the AMNH departed from today's usual hurdles of open competitive searches, short lists, and job seminars. While Guy was mired in analyzing data and writing his thesis, Burt and Hooper began nudging him to think about future job possibilities. Given his overriding interests in museum-based field investigation and having a somewhat loner personality, Guy never pictured himself teaching in an academic setting, surrounded by a stable of graduate students. Instead, he recalled the feelings of grand adventure instilled when, as a grad student at Utah, he first perused AMNH bulletins on the early Archbold New Guinea expeditions. Based on such stray recollections, Guy decided that the AMNH would be a neat place to work and enjoined Hooper to write Richard Van Gelder, then chairman of the AMNH Department of Mammalogy, and inquire about curatorial positions for a soon-to-graduate prospect. Hooper's first inquiry elicited a "Don't call us, we'll call you" response... and shortly afterward they did.

The impending retirement of Leonard J. Brass, Archbold Associate Curator and the chief botanist on the New Guinea expeditions, prompted Van Gelder to reconsider and contact Hooper about his student's qualifications and depth of interest. An abrupt trip to New York City, an introduction to the department and collections, and dinner with Van Gelder and Brass culminated with an on-the-spot job offer from Van Gelder. Although this serendipitous cascade of events nowadays borders on the unbelievable, history would judge that the individual's experience and talents preeminently suited the position's requirements and expectations.

AMERICAN MUSEUM OF NATURAL HISTORY (1966–2002)

Guy joined the Department of Mammalogy in 1966 before completing his Ph.D. thesis. Hooper afterward confessed a nagging worry that Guy's premature departure for a curatorial plum in an elite museum would erode or erase any initiative to finalize his doctoral research, thereby following the path of certain other Michigan graduate students in mammalogy (notably, C.O. Handley, Jr., an earlier Hooper student who left to become a curator in the U.S. National Museum in 1949, but did not finish his dissertation until 1955). Hooper's concern was misplaced. While Guy was familiarizing himself with his new AMNH colleagues and the extensive mammal collections, he diligently refined the *Sciurus aureogaster* study, returned to Michigan in 1967 to formally file his dissertation, and submitted it to the UMMZ series soon thereafter (9).

The AMNH position offered to Guy was that of Archbold Assistant Curator, a curatorship funded by one of the Museum's major benefactors, Richard Archbold. Archbold (1907–1976) was independently wealthy, the family's riches stemming from early ventures in Pennsylvania oil refineries, and throughout his lifetime he sought meaningful avenues to disperse that wealth, including geographic exploration and natural history discovery. In the 1930s, Archbold sponsored a series of AMNH expeditions, personally leading those to New Guinea but also supporting collectors in Sulawesi (Celebes) and northern Australia, where the field teams broadly collected vertebrates, insects, and plants. As a research associate in the Department of Mammalogy (1931–1976), Archbold participated in many of the mammalian descriptions emanating from these expeditions, especially those authored in collaboration with George Tate, the expedition's lead mammalogist (e.g., Tate and Archbold, 1935). Archbold's scientific philanthropy was soon incorporated as the nonprofit Archbold Expeditions, a bountiful partnership that supported Museum fieldwork and personnel costs during the years 1937–1981. The titles in many of Guy's publications accordingly include the preface "Results of the Archbold Expeditions, No. *x*," and after Archbold passed away, he honored the man for his "patronage and commitment to indifferent inquiry" by naming a new genus of Philippine murid (*Archboldomys* Musser, 1982). Archbold's sister, Frances Archbold Hufty, continued as president of Archbold Expeditions after her brother's death, but financial support for the Museum dwindled and eventually ended in 1981. Guy nonetheless preferred to retain the honorary title of Archbold Curator until his retirement, the last of a distinguished line of AMNH Archbold curators.

Taxonomic Themes and Research Approach

> When I began writing papers about rats it became very clear that what most of the literature on murid systematics lacked was stated context and reasons why the papers were necessary. The systematic sections are really very boring to most readers, even mammalogists. But, to put the results in some kind of context, either evolutionary or historical, adds significant dimension and, depending on the competence of the section, depth. I think that this combination of data analyses, results, and context is what defines scholarship. (GGM, in litt., 15 July 1998).

Guy's concept of scholarship is plainly evident in the 108 scientific papers that he has produced to date, a publication record notable for its uniformly high quality and steady productivity that features the regular

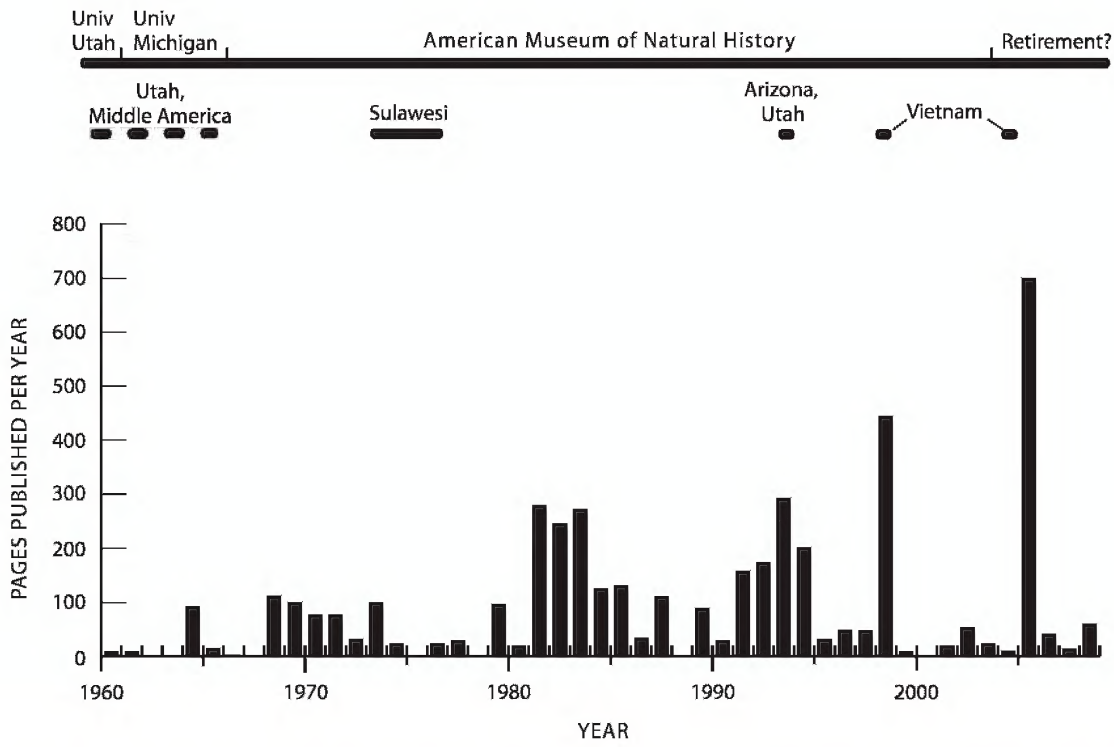

Fig. 1. Three perspectives that summarize broad aspects of Guy G. Musser's professional career. The top bar brackets institutional bases where he conducted his museum researches; the interrupted lower bar indicates general areas where fieldwork was periodically conducted. The histogram views his career productivity in terms of pages published per year (see appendix 1). From his earlier contributions that treated alpha taxonomic details of *Peromyscus* and *Rattus*, among others, his publications have trended toward larger, more synthetic revisions, monographs, and taxonomic catalogs.

appearance of monographic treatises (appendix 1, fig. 1). The majority of his papers (80 publications) involve taxonomic descriptions and revisions of muroid rodents, by far the most speciose superfamily of living mammals (e.g., Wilson and Reeder, 2005), and as a body of work, his contributions have substantially reordered our systematic understanding of these diverse rats and mice from the species to family ranks. Guy's research on Muroidea has emphasized genera and species of Old World muroids (Muridae: Murinae [61 publications]), pursuant to his responsibilities as an Archbold curator, and to a lesser extent certain New World groups (Cricetidae: Neotominae [6 publications] and Sigmodontinae [7 publications]) and higher-order classifications of the superfamily (5 publications). These broad taxonomic foci and the research effort dedicated among them are approximately reflected in the impressive numbers of new mammalian taxa that Guy has described—including 2 subspecies, 39 species, 19 genera, 3 tribes, and 2 subfamilies—over the period from 1961 through 2009 (and counting; table 1). Such parameters outline the bare results of his lifelong researches but say little about their context and impact.

Indo-Australian Muroids (Murinae): Upon Guy's arrival at the AMNH as a newly minted Archbold Assistant Curator, there already existed a rich collection of mammals from the Indo-Australian region that invited careful research, as well as a mechanism, the Archbold Expeditions, Inc., that encouraged pursuit of museum and field studies relating to them. From this stage, his research focus and publication theme are largely straightforward.

Guy's early years at the AMNH were spent learning the mammals, especially Ro-

TABLE 1
New Taxa (in boldface) described by Guy G. Musser and Colleagues
(Arranged chronologically and grouped by family and country or broad geographic region. † = fossil taxon; * = genus or species based on new material collected by Musser or coauthors; no symbol = genus or species based on old material reposing in collections from 20–100 years.)

Taxon, Authorship, and Year	Geographic Domain
Neotropical Sciuridae:	
Glaucomys sabrinus* ***murinauralis* Musser, 1961	United States
Neotropical Cricetidae:	
Habromys[a] Hooper and Musser, 1964b	Mesoamerica
Isthmomys[a] Hooper and Musser, 1964b	Panama
Osgoodomys[a] Hooper and Musser, 1964b	Mexico
Peromyscus thomasi* ***cryophilus*[b] Musser, 1964	Mexico
Peromyscus* ***chinanteco* Robertson and Musser, 1976	Mexico
Daptomys* ***peruviensis*[c] Musser and Gardner, 1974	Peru
Oryzomys ***tatei*** Musser, Carleton, Brothers, and Gardner, 1998	Ecuador
Oryzomys* ***emmonsae* Musser, Carleton, Brothers, and Gardner, 1998	Brazil
Oecomys* ***sydandersoni* Carleton, Emmons, and Musser, 2009	Bolivia
Indo-Australian Muridae:	
Tateomys rhinogradoides Musser, 1969b	Sulawesi
Chiropodomys ***karlkoopmani*** Musser, 1979	Sumatra
Komodomys Musser and Boeadi, 1980	Lesser Sundas
Srilankamys Musser, 1981a	Sri Lanka
Margaretamys Musser, 1981a	Sulawesi
M. **elegans* Musser, 1981a	Sulawesi
M. **parvus* Musser, 1981a	Sulawesi
Anonymomys mindorensis Musser, 1981a	Philippines
†*Papagomys* ***theodorverhoeveni*** Musser, 1981b	Lesser Sundas
†***Hooijeromys nusatenggara*** Musser, 1981b	Lesser Sundas
†***Paulamys naso***[d] Musser, 1981b	Lesser Sundas
Kadarsanomys Musser, 1981c	Java
Rhynchomys ***isarogensis*** Musser and Freeman, 1981	Philippines
Crateromys ***paulus*** Musser and Gordon, 1981	Philippines
Abditomys Musser, 1982a	Philippines
Crunomys ***rabori***[e] Musser, 1982c	Philippines
Crunomys* ***celebensis* Musser, 1982c	Sulawesi
Archboldomys luzonensis Musser, 1982c	Philippines
Tateomys* ***macrocercus* Musser, 1982c	Sulawesi
Hydromys ***hussoni*** Musser and Piik, 1982	New Guinea
†*Rattus* ***trinilensis*** Musser, 1982d	Java
Palawanomys furvus Musser and Newcomb, 1983	Palawan
Sundamys Musser and Newcomb, 1983	Sunda Shelf
Rattus ***osgoodi*** Musser and Newcomb, 1985	Vietnam
Rattus ***tawitawiensis*** Musser and Heaney, 1985	Philippines
Crateromys* ***australis* Musser, Heaney, and Rabor, 1985	Philippines
†*Hadromys* ***loujacobsi*** Musser, 1987a	Pakistan
Bunomys* ***prolatus* Musser, 1991	Sulawesi
Maxomys* ***wattsi* Musser, 1991	Sulawesi
Rattus ***koopmani*** Musser and Holden, 1991	Sulawesi
Tarsomys ***echinatus*** Musser and Heaney, 1992	Philippines
Batomys* ***russatus* Musser, Heaney, and Tabaranza, 1998	Philippines
Sommeromys macrorhinos Musser and Durden, 2002	Sulawesi
*****Saxatilomys paulinae*** Musser, Smith, Robinson, and Lunde, 2005	Lao PDR
*****Tonkinomys daovantieni*** Musser, Lunde, and Son, 2006	Vietnam
Leptomys ***paulus*** Musser, Helgen, and Lunde, 2008	New Guinea

TABLE 1
(Continued)

Taxon, Authorship, and Year	Geographic Domain
Leptomys ***arfakensis*** Musser, Helgen, and Lunde, 2008	New Guinea
Coccymys ***kirrhos*** Musser and Lunde, 2009	New Guinea
Brassomys Musser and Lunde, 2009	New Guinea
Muroidea:	
Delanymyinae Musser and Carleton, 2005	Africa
Leimacomyinae Musser and Carleton, 2005	Africa
Baiomyini Musser and Carleton, 2005	North America
Ochrotomyini Musser and Carleton, 2005	North America
Nyctomyini Musser and Carleton, 2005	Middle America
Asian Soricidae:	
Chodsigoa ***caovansunga*** Lunde, Musser, and Son, 2003	Vietnam
Crocidura ***kegoensis*** Lunde, Musser, and Ziegler, 2004	Vietnam
Suckling lice (Anoplura):	
Hoplopleura ***traubi*** Durden and Musser, 1991	Sulawesi
Polyplax* ***melasmothrixi* Durden and Musser, 1992	Sulawesi
Hoplopleura ***sommeri*** Musser and Durden, 2002	Sulawesi

[a] Described as subgenus.
[b] Elevated to species by Carleton (1989).
[c] Now = *Neusticomys peruviensis* sensu Voss (1988).
[d] *Paulamys* Musser (1986) was coined as a replacement name for *Floresomys* Musser, 1981.
[e] Merged as a junior synonym of *Crunomys melanius* by Rickart et al. (1998).

dentia, of the region, and assessing the strengths and weaknesses of the collections. This education necessarily required much basic, hands-on curation, bringing a peromyscine yardstick of discrimination to the murine identifications and alpha taxonomies of Archbold and Tate. Guy also invested considerable curatorial effort in the important Indo-Malayan rodent series contained in the U.S. National Museum of Natural History (USNM), the repository of collections generated by W.C. Abbott and H.C. Raven, along with the numerous holotypes and type series of taxa described by Ned Hollister and Gerrit Miller in the early 1900s (e.g., Miller, 1900; Hollister, 1913; Miller and Hollister, 1921). In the late 1960s through early 1970s, Guy worked so often in the USNM, commuting by rail between New York City and Washington, D.C., that the divisional technicians viewed him as the Mammal Division's fourth curator.[4] Having improved the identification of material housed in North American collections as a dependable taxonomic resource, travel to European museums was the obvious next step. Those that contained critical series of Indo-Australian rats and mice—the British Museum of Natural History, London (BMNH); Rijksmuseum van Natuurlijke Histoire, Leiden; and the Museum National d'Histoire Naturelle, Paris—were visited in 1969, not as a routine museum trip of days to weeks in duration but a prolonged tour of five months.

> The British Museum and the museum at Leiden are full of real treasures. Going through their collections is like being in the field and discovering new and interesting animals. (GGM, in litt., 2 February 1970)

Examination of holotypes and associated material, the bases of descriptions by early workers such as Oldfield Thomas, F.A.

[4] In the late 1960s, curators in the USNM Division of Mammals included Charles O. Handley, Jr. (1949–2000), David H. Johnson (1941–1967), and Henry W. Setzer (1948–1978). By the early 1970s, Johnson had retired and the Division expanded to include Handley, Setzer, James Mead (Marine Mammal Program), and Richard Thorington (Primates Program). Technically, Guy would have been the "fifth" USNM curator over this period.

Jentink, and Alphonse Milne-Edwards, was necessary to resolve explicit nomenclatural problems and enlighten taxonomic suspicions. By the conclusion of the 1969 European trip, he had examined all of the types of rodent taxa known from Sulawesi. A three-month museum trip followed in 1971 to study collections in Indonesia, Malaya, Singapore, and Thailand.

The dividends from this initial phase of museum investigation started to appear in papers produced from 1969 to 1973 (appendix 1). The majority of these focused on taxa described from Sulawesi and most involved reparatory taxonomic and nomenclatural issues: providing diagnoses and comparisons for obscure taxa; resurrecting epithets long buried in *Rattus* infraspecific taxonomy to valid species; reassigning subjective synonyms among species judged to be valid, especially the allocation of poorly known forms with the correct species of commensal *Rattus*; emending definitions of taxa based on composite holotypes, designating lectotypes, and restricting type localities. In one exceptionally contorted case (17), the type series of *Mus callitrichus* Jentink, 1879, proved to be a mixture of five divergent species (*Taeromys callitrichus* proper plus *Bunomys chrysocomus*, *B. fratorum*, *Pauromys dominator*, and *Rattus hoffmani*). Only one new taxonomic description appeared in this period (*Tateomys rhinogradoides* Musser, 1969), but "Results of the Archbold Expeditions. No. 91" was a beefy *Novitates* (12) that portended the succession of insightful AMNH reports and monographs on Indo-Australian murids. Hooper chuckled that only Guy could write a 41-page article based on a single specimen. Of course, the paper covered much more than an exacting morphological description of *Tateomys* (which it certainly contained), but it also broadly addressed evolutionary origins and possible relationships among the shrew rats of Sulawesi and the Philippines and began to consolidate the rodent genera endemic to Sulawesi. Those uninitiated to the arcana of murine nomenclature may find such papers tortuous to read, yet together they constituted the building stones of an objective foundation that would impel a fresh look at the diversification of murine rodents across the Indo-Australian region. A crucial aspect of any fresh look would depend upon renewed biological survey.

> Spent a week with Musser at AMNH. Good for the soul. The museum thinks he will be gone for a year. He thinks 3 years. (D.J. Klingener, in litt., 5 July 1973)

And three years it was: from June 1973 to September 1976, Guy lived in the forests of Sulawesi and accumulated a superb collection of small mammals, especially rodents. As a Michigan grad student at the time, I kept writing to AMNH to inquire when Musser would return from Sulawesi, only to learn that he had extended his fieldwork for still another six months in view of the exciting discoveries being made. Van Gelder and Sydney Anderson, departmental chairs during those years, didn't seem to mind his prolonged absence in view of the shipments of well-preserved small mammals that periodically emerged from somewhere in the forests of Sulawesi, with runners porting specimens out and carrying supplies in as required, all shipped via Jakarta. Guy purposefully situated his base camps in primary forests of the interior, away from human settlements, and concentrated his field surveys in the central highlands of Sulawesi. Detailed altitudinal transects from lowland evergreen rainforest through upper montane rainforest were regularly established to delimit altitudinal ranges and ecological occurrences (e.g., see Musser and Holden, 1991 [71]: table 18). The value of his Sulawesian collections is enhanced not only by the quality of the specimen preparations but, for the era, their variety—yes, the traditional skins and skulls, but also fluids, skeletons, and chromosomal preparations ("I can now run rats through the chromosome mill and that required a whole different suite of junk that I am unused to taking into the field."—GGM, in litt., 5 June 1973). Reams of ecological, reproductive, and dietary information were recovered and habitats and live animals were photographed in order to document the natural history of the specimens collected. The latter kinds of data were typically absent from the scanty descriptive literature with which Guy had to contend, but they would be profusely integrated throughout his subsequent generic and specific revisions.

> I don't think that I could stand to do something else like this [1979 study of *Chiropodomys*] for a while, but then these papers always start out innocently and innocuously; I am still perplexed why this one grew into a monster. (GGM, in litt., 19 April 1978)

At a girth of merely 69 pages, the *Chiropodomys* revision (35) would prove to be only a dwarf Godzilla compared with the monographic monsters that were soon to hatch. The continuing dissemination of results from Guy's museum sleuthing, now supplemented by the abundant new material collected during his Sulawesian expedition, would yield a fertile second phase of publication on murine systematics (1979–1987; appendix 1, fig. 1). The majority of his murine descriptions, 11 genera and 20 species, appeared during this period (table 1), which included five substantial *Bulletins*, many weighty *Novitates*, and some of the longest "notes" ever published in *Journal of Mammalogy* before the journal abandoned that subdivision of articles. Such numbers of taxa new to science pale against the lifetime output of a C. Hart Merriam (U.S. Biological Survey) or Oldfield Thomas (BMNH), but one must appreciate that Guy's mammalian discoveries transpired in the latter 1900s, a century after the inception of directed survey collecting and correlative eruption of taxonomic description (e.g., Kohler, 2006). For someone whose command of the Eurasian and Indo-Australian murid faunas was now so expert, new species or genera were relatively simple to spot in a drawer of specimens (though proper documentation of those novelties was never a simple task). More taxonomically complicated and excruciating to document were the many groups extricated from the nebulous construct and bloated synonymy of Indo-Australian *Rattus* that prevailed in the middle 1900s (e.g., Chasen, 1940; Ellerman, 1941, 1961; Simpson, 1945; Ellerman and Morrison-Scott, 1951; Tate, 1951; Laurie and Hill, 1954). Genera such as *Limnomys* (34), *Maxomys* (37), *Leopoldamys* and *Niviventer* (40), *Apomys* (46), and *Berylmys*, *Bullimus*, and *Bunomys* (52) had to be differentiated from *Rattus* and from one another, their morphological diagnoses recrafted, and their specific contents and distributions redefined.

Guy's contributions to the systematics of Indo-Australian murines have steadily continued from 1990 onward (appendix 1), but not with the concentrated flourishes that characterized the two earlier periods. Preoccupation with new research interests competed for his time and energy. Noteworthy over this latter period was the 1992 monograph of Musser and Heaney on native Philippine murines (74). Though not a quantitative phyletic analysis per se, the authors systematized the character variation among the 18 native genera as evidence of three major divisions and developed phylogenetic and biogeographic hypotheses to account those divisions. A recent molecular study (Jansa et al., 2006) has broadly supported their ideas, particularly with regard to Old Endemic and New Endemic groupings, although disagreeing (naturally) over details. Guy twice returned to the field in the Indo-Australian region, in 1998 and 2004, after a lapse of 22 years since the productive expedition to Sulawesi. Field trips of 1–2 months duration were conducted to Vietnam, under the auspices of the AMNH Center for Biodiversity and Conservation, and uncovered new species of shrews and a new genus and species of rodent (96, 99, 104; table 1). Guy coordinated the first Vietnam trip, but Darrin Lunde, a frequent collaborator and AMNH Collection Manager of Mammals, handled all logistics for the second, with Guy tagging along as earnest field hand (fig. 2).

> He knew I was going to Vietnam and after I had already made the necessary arrangements, Guy mentioned that he really missed going into the field.... He just wanted to trap.... Needless to say he was one of the most amazing field assistants anyone ever had, and it was a role he seemed to fill with great humor. I remember him gloating every time I had... to deal with permits or any number of other unpleasantries you need to take care of in the field. He would just pick up some traps to head off into the forest with what seemed an almost gleeful smile. (D.P. Lunde, in litt., 25 September 2008)

Guy's studies of Indo-Australian murines feature twin subtexts that are threaded among the bare bones of his taxonomic findings and amended synonymies. One was the need to disentangle truly indigenous

Fig. 2. Twenty-two years after his fieldwork in Sulawesi (see frontispiece), Guy returned to fieldwork in Indo-Malayan forests, this time for shorter surveys conducted in Vietnam in 1998 and 2004. Guy is pictured here with a live individual of the new genus and species *Tonkinomys daovantieni* Musser, Lunde, and Son, 2006 (photograph by Darrin P. Lunde, 2004). When a live animal was captured, Guy often retained it in the trap in order to observe its behavior and to test reactions to various foodstuffs.

species from those forms associated with human peregrinations and agricultural activities. Credible identification of the latter (commensal) species was hindered by an overburden of scientific names, particularly for *Rattus*, and the consequent nomenclatural morass obscured real biogeographic commonalities or differences among the murine faunas of Sulawesi, the Philippines, and Sunda Shelf (fig. 3). The 1973 paper on *Rattus argentiventer* (28), the ricefield rat once considered to be an ecological subspecies of *R. rattus*, signaled his emerging perception of the microdistributional dichotomy between indigenous murines (mainly confined to pristine environments) and introduced species (limited to anthropogenic settings), and other reports followed to solidify this pattern (33, 52, 63, 71). Other researchers had appreciated such a division, albeit on a local basis (e.g., Barbehenn et al., 1972–1973, for the Philippines). Guy grounded his morphological understanding of commensal species through actual examination of type specimens; periodically updated the growing list of synonyms, many described and long disguised as endemic species (especially see 33, 52); and achieved a fresh picture of their distributions throughout the Indo-Australian region. These dogged efforts revealed a surprisingly diverse suite of species that are never encountered in primary forest (apart from the usual triumvirate of *Rattus rattus*, *R. norvegicus*, and *Mus musculus*), and whose presence on the Sunda Shelf or across Indo-Australian island groups had resulted

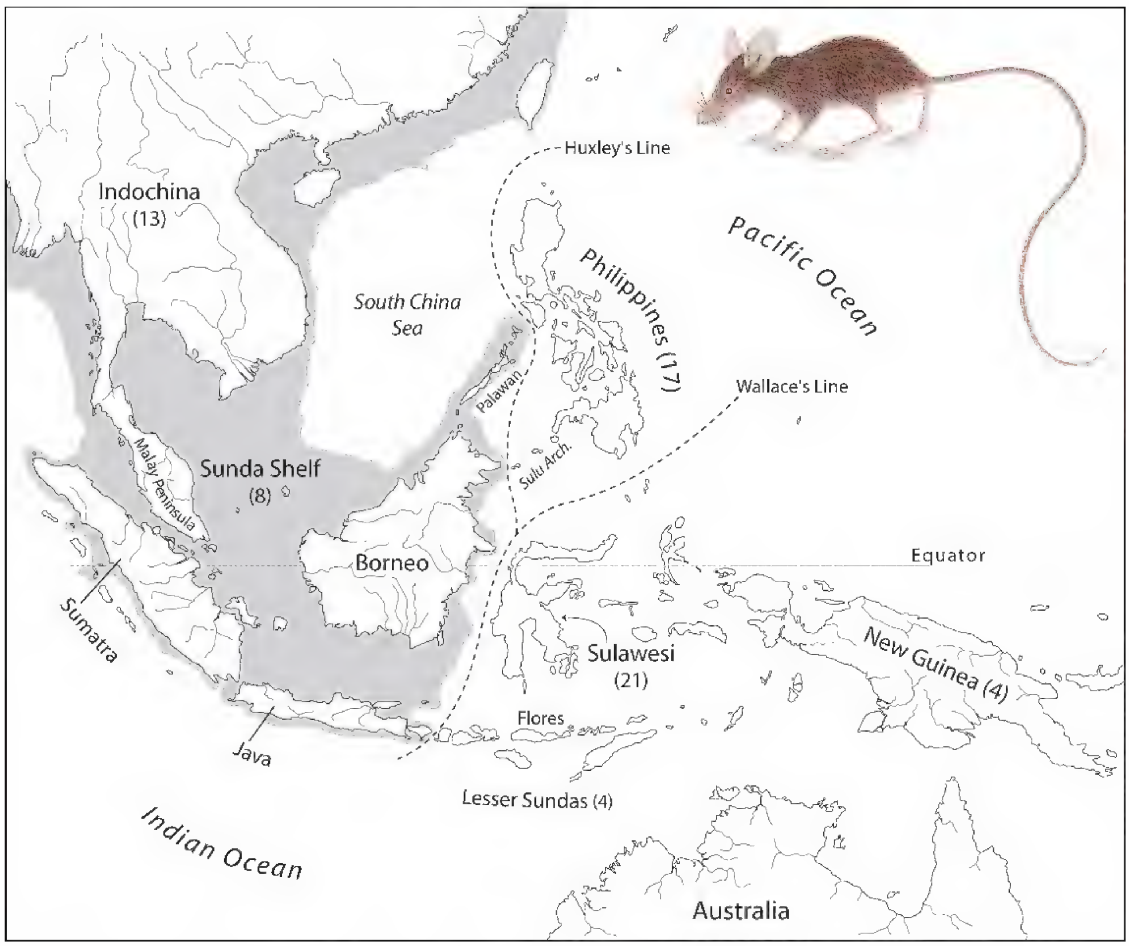

Fig. 3. The Indo-Australian region formed the dramatic geographic backdrop to Guy G. Musser's systematic studies of Murinae. Sulawesi, where Guy spent three years in the field (1973–1976), was the centerpiece of his contributions to murine systematics, but substantial research was necessarily devoted to nearby islands, archipelagos, and Indochina to clarify the taxonomy, evolutionary relationships, and biogeography of rats and mice that inhabit the region (numbers in parentheses next to island groups or geographic feature signify the number of publications that principally address taxa in those areas). Color inset: *Sommeromys macrorhinus* Musser and Durden (2002), one of the many endemics described from Sulawesi (drawing by Patricia Wynne). (Figure adapted from Musser, 1981[40].)

from human-mediated introductions (i.e., *R. argentiventer*, *R. exulans*, *R. nitidus*, *R. tanezumi*, *Bandicota indica*, *B. bengalensis*, *Mus caroli*, *M. cervicolor*, and *M. terricolor*). Coincidentally, the degree of endemism recorded for indigenous rodents was substantially enhanced at both specific and generic ranks. The taxonomic lists and endemism tallies for various Indo-Malayan island groups presented in a recent article on the "Diversity, distribution, and conservation of endemic island rodents" readily attest to the magnitude of Guy's alpha-taxonomic labors (Amori et al., 2008; also see, Corbet and Hill, 1992).

The second interwoven subtext concerned the need for a morphologically credible, monophyletic construct of the genus *Rattus*. The heterogeneous, waste-basket composition of the genus handed down from the era of Chasen, Ellerman, and Simpson defied objective diagnosis, and its apparently expansive occurrence across the Indo-Australian region posed distributional enigmas that misled past

zoogeographers. Misonne (1969) began to unravel this view of *Rattus* by excluding genera endemic to Africa, but little headway had been accomplished with Indo-Malayan rodents when Guy started to work with the Archbold collections. His approach to the problem was direct and methodical: sorting out clearly definable, morphological clusters; describing new genera (table 1) or resurrecting genus-group taxa uncritically lumped under *Rattus* (e.g., 37, 39, 52); and contrasting all of these with regional forms of true *Rattus*. Most generic changes were accompanied by detailed enumerations of differentiating traits and/or tabulations of primitive versus derived character states (such as, 39, 52, 71, 74). By the close of his second phase of murine investigations in 1987, Guy could record that the indigenous murines on Sulawesi consisted of 14 genera and 36 species, four of them in *Rattus* (63); in contrast, Laurie and Hill (1954) had recognized six genera and 35 species, 29 of them in *Rattus*. Although the process was operationally phenetic, the ultimate goal was phylogenetic. His taxonomic amendments typically raised evolutionary questions that invite testing and identified explicit means to reject or accept his proposals. Recent molecular studies of murine phylogeny appear to offer broad support for his redrawn limits of genera and notions of relationship vis-à-vis *Rattus* (e.g., Steppan et al., 2005; Jansa et al., 2006; Lecompte et al., 2008; Rowe et al., 2008). Forms such as *Apomys*, *Maxomys*, and *Sundamys* decidedly fall outside the clade of *Rattus* proper, and the polyphyletic burden of the genus sensu Ellerman and others has been appreciably and irrevocably reduced. Throughout his ongoing murine investigations, Guy had obviously formulated a working diagnosis of *Rattus* sensu strico and intended one day to punctuate his many alpha-taxonomic projects with a proper phylogenetic delineation of the genus. As sometimes happens, one's ambitions run out of lifetime to fulfill them.

Guy would not style himself as a biogeographer, but his research arguably holds its greatest relevance within the arena of Indo-Australian biogeography. Still, encamping for three years in the forests of Sulawesi speaks an awareness of biogeographic insights that could unfold from intense fieldwork there. Sulawesi is a large island found immediately east of Wallace's line (fig. 3), where so many abrupt faunal and floral changes are recorded compared with islands of the Sunda Shelf and the Philippines, and is situated at the nexus of colliding tectonic plates and complex geomorphic changes. The study group of choice, murine rodents, also conveys a deliberate calculation in view of their low vagility, the ample opportunities for fine-grained speciation across such a geologically volatile region, and the general want of rigorous revision since the descriptive era. Yet only a couple of his papers overtly address murine biogeography of the region (33, 63). Instead, most remarks on the topic are relayed incidentally within his revisions and descriptions, which also consider the biogeographic ramifications of the proposed taxonomic changes and summarize the altered picture of faunal associations and endemism patterns. A noteworthy example was the description of *Rattus osgoodi* from southern Vietnam (56), a paper that highlighted the Annamite Mountains as an area of endemism before the biogeographic excitement they sparked apropos the discovery of new ungulates (Dung et al., 1993; Giao et al., 1998). His studies of fossil and subfossil murines (late Pliocene–Holocene) from Sulawesi and various Lesser Sunda Islands have supplied another important window to understanding the paleogeography of the region (40, 48, 53, 90, 91).

In the context of assessing rates of extinction and colonization in southeastern Asia, Heaney (1986) pleaded "for research of the most fundamental sort. All of these [biogeographic] studies are predicated on the availability of accurate taxonomic data, and yet the distributions and systematic relations of many, if not most, insular mammals are poorly known, especially in the tropics. Theoretical advances in island biogeography are currently impeded by insufficient empirical data." In effect, Guy's career of thoughtfully crafted systematic essays was undertaken with just those inadequacies foremost in mind. Looking back, the conceptual landscape that existed when Guy initiated his researches on Indo-Australian rodents resembled, in geographic and taxonomic scale, the state of sigmodontine

taxonomy as direly assessed by Ellerman (1941: 327): "But directly Panama is passed, an enormous list of names described for the most part binomially, and in appalling chaos, is reached." If one rephrased this as "But directly the Malay Peninsula is passed," Ellerman's words would capture the systematic confusion that greeted the young Archbold Assistant Curator in 1966.

New World Muroids (Neotominae and Sigmodontinae): Among the small mammals collected in the Tushar Mountains of southwestern Utah, Guy was certainly drawn to the variety of native muroid rodents (Neotominae) and intrigued by the difficulties in supplying specific determinations. He developed a fondness for woodrats and fleetingly considered *Neotoma* as a research focus, but the move to UMMZ cemented his interest in the systematics of *Peromyscus*. Presented with the opportunity to work with an eminent "peromyscologist," how could it have happened otherwise? When not hunting for tree squirrels in southern Mexico (1963–1965), Guy managed to set and run traplines, yielding catches of interesting *Peromyscus*. These specimens provided the impetus for important reports on the taxonomy and distribution of a wide array of Neotropical groups, notably those of *P.* (*Megadontomys*) *thomasi* (6), *P.* (*Osgoodomys*) *banderanus* (10), the *P.* (*Habromys*) *lepturus* complex (10, 32), and the *P. mexicanus* group (6, 10, 20). Undoubtedly the most influential of his *Peromyscus* researches was the 1964 collaboration with his major professor (5). "Notes on Classification" expanded upon Hooper's (1958) application of male reproductive anatomy to evaluate interspecific relationships and formal groupings within the genus, and together they conceived the most substantive reclassification into species groups and subgenera (some newly described; see table 1) since Osgood's (1909) classic work. The 1964 paper set the stage for Hooper's (1968) deft review of *Peromyscus* classification, and together they have animated four decades of fruitful and penetrating research, drawing upon a variety of data, analytical tools, and research methodologies (e.g., see many articles cited in Carleton, 1989, and in Musser and Carleton, 2005 [103]). To judge from recent issues of *Journal of Mammalogy,* the discussion continues (Bradley et al., 2007; Miller and Engstrom, 2008).

> You know I have always enjoyed working with *Peromyscus*, especially groups that are so diverse, like the *mexicanus* bunch. Sometimes I feel like chucking *Rattus* and going back to Mexico and Central America. (GGM, in litt., 6 October 1977)

The unrelenting tug to first complete his Indo-Australian projects effectively stifled such passing yearnings for a taxonomic first love.

However, Guy's research sights did turn once more to New World rodents, this time drawn to the impressive radiation of South American cricetids (Sigmodontinae). Besides presenting the opportunity to work with a valued colleague, the description of a new ichthyomyine species (31) with Al Gardner dovetailed with Guy's planned revision of the ichthyomyine group, a project earlier initiated by Hooper and continued by Guy when he relocated to the AMNH. Aware that he could never finish a thorough review as his Indo-Australian projects proliferated, Guy returned his ichthyomyine loans in 1977. Another UMMZ student of a successive generation would carry forth investigation of the group and resoundingly close a circle of sorts (Voss, 1988). More taxonomic attention was devoted to another tribe of Sigmodontinae, the Oryzomyini (55, 64, 65, 85, 89, 107). The genesis of these papers stemmed from basic curation of the large oryzomyine holdings in the AMNH and USNM, a task that exposed the glaring inadequacies of species definitions and generic limits as then recognized (notably, Goldman, 1918; Hershkovitz, 1960; Cabrera, 1961; Handley, 1976). The impediments to improve understanding of oryzomyine diversity somewhat paralleled the situation that Guy encountered when first grappling with Indo-Australian murines: an abundance of names used inconsistently for decades and lack of a phylogenetic diagnosis of *Oryzomys* sensu stricto. The deconstruction of the polyphyletic mishmash that so long characterized *Oryzomys* was precipitated by the watershed karyotypic paper of Gardner and Patton (1976), advanced by the studies of Carleton and Musser (1989 [65]) and Musser et al. (1998 [89]), and completed

by the syncretistic investigations of Weksler (2006; Weksler et al., 2006). During the years of reidentifying oryzomyine specimens, Guy predictably called upon those same discriminatory abilities acquired through his early *Peromyscus* examinations, as exemplified by his remarks on researching the *Oligoryzomys* addendum to our *Microryzomys* revision (65).

> It has been very rewarding. *Oligoryzomys* turns out to be much like *Peromyscus* and once you adjust the neurons to *Peromyscus* receptors, the species of *Oligoryzomys* jump out at you. I am wondering why others did not see the patterns earlier. (GGM, in litt., 25 January 1989)

Muroid Rodent Classification and Relationships: Guy's interest in relationships among muroid lineages was whetted by his experience as research assistant to Hooper in the early 1960s. Their morphological survey of "The glans penis in Neotropical cricetines" formed a framework for reassessing relationship, in this case higher levels of kinship among neotomine-peromyscines (Neotominae), South American cricetines (Sigmodontinae), and major assemblages of Muroidea (4). The 1964 study of Hooper and Musser immediately drew sharp criticism from Hershkovitz (1966) for recklessly drawing broad phylogenetic conclusions based on a single organ (Karl Koopman occasionally tweaked Guy by reciting one of Hershkovitz's more colorful lines—namely, that their study was "insistently and unremittingly phallic and typological," a quotation punctuated by Karl's peals of laughter). Notwithstanding Hershkovitz's caustic disapproval, the 1964 report (4) has stimulated vigorous and abundant follow-up research, including taxonomically broad surveys of other organ systems (Carleton, 1973; Voss and Linzey, 1981) and phylogenetic studies using morphological characters (Carleton, 1980; Steppan, 1995). In particular, their diagrams of possible relationships, at the generic and family level (e.g., see fig. 4), were sufficiently explicit to provoke testing by that new information base for phylogenetic inference, DNA sequences (e.g., Engel et al., 1998; Smith and Patton, 1999, Michaux et al., 2001; D'Elía 2003; Bradley et al., 2004; Jansa and Weksler, 2004; Steppan et al., 2004). True, Hooper and Musser did not supply an OTU by character-state matrix, branch-support statistics, or consensus trees, but their diagrams did depict evolutionary lines of descent and hierarchies of relationship. Viewed against the long sweep of muroid classifications, from Gill (1872) to Musser and Carleton (2005 [103]), the innovative studies of Hooper and Musser (4, 5) served as conceptual stepping stones between the evolutionary taxonomy of Mayr and Simpson and the phylogenetic systematics of Hennig and its various quantitative phyletic applications.

The 1984 review of muroid rodents (54) unfolded from Anderson's appeal to Guy for recommendations of authors who could assume responsibility for orphaned chapters from the first edition (Anderson and Jones, 1967). Although our collaboration was faulted for equivocation over the issue of Cricetidae versus Muridae (Hershkovitz, 1993), a reclassification of Muroidea was never the chapter's purpose (Carleton and Musser, 1984 [54]: 300): "Consequently... our arrangement of the groups as equivalent subfamilies of Muridae reflects not our conviction that this is the preferred nomenclature, but rather our uncertainty of the hierarchical pattern and our desire to focus upon the distinctive and richly varied geographic and biological properties of the groups comprising the Muroidea." Based on extensive specimen examination and literature search, traits used to diagnose muroid groups were evaluated as primitive versus derived character states, amplified, and discussed in terms of the evidence for monophyly, patterns of relationship, and support for past classifications. With regard to these more modest aims, the chapter succeeded and provided the family-group rationale adopted in Guy's subsequent contributions on the superfamily (78, 87).

When Don Wilson became Chair of the American Society of Mammalogists Checklist Committee in 1990, he initiated important format changes for preparation of the next editions of Mammal Species of the World (Wilson and Reeder, 1993, 2005). Foremost, it was agreed that individual authors would be recognized for each family, rather than buried among some 150 contributors in a forgotten preface as was done for the first edition (Honacki et al., 1982). This change

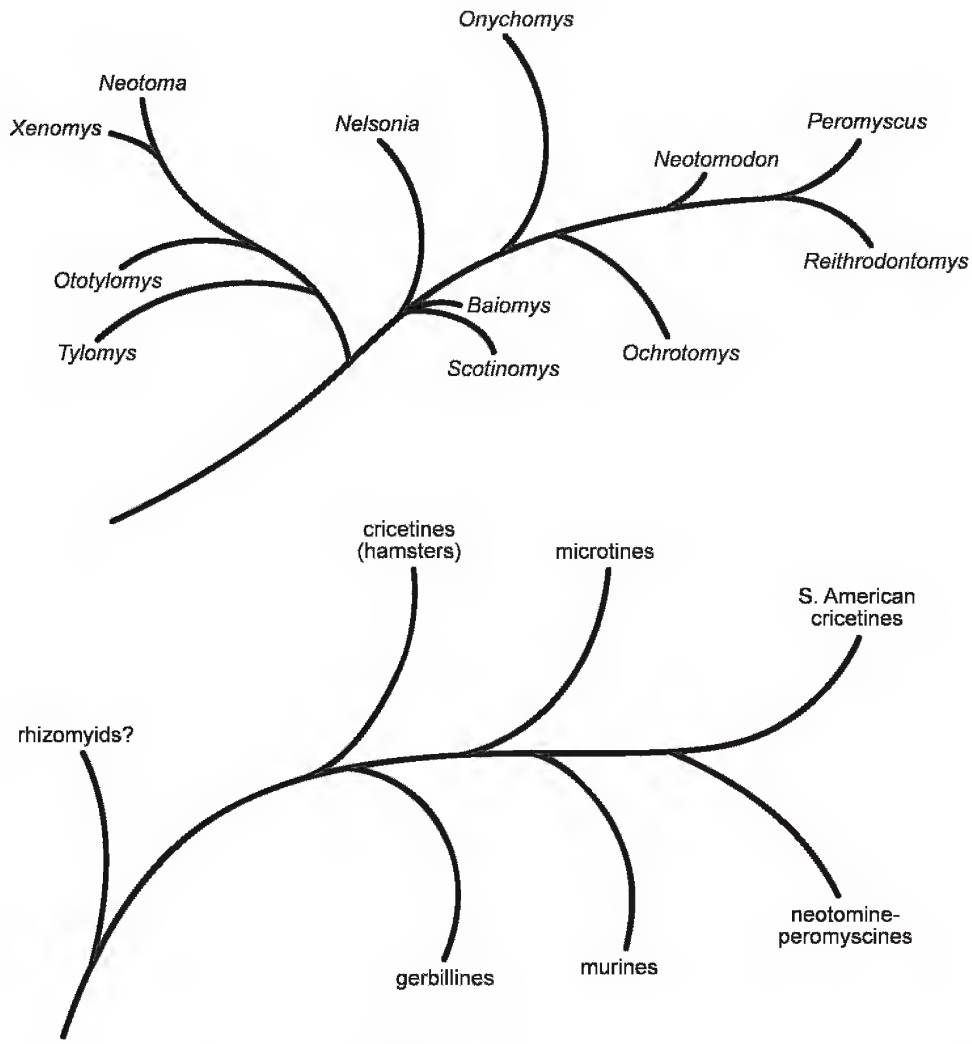

Fig. 4. Two diagrams of possible relationships developed by Hooper and Musser as based on their morphological surveys of the glans penis in various assemblages of muroids. **Top**, hypothesized phyletic affinity among genera of neotomine-peromyscines (Neotominae); **bottom**, hypothesized relationships among several groups (subfamilies) of Muroidea (after Hooper and Musser, 1964[4]: figs. 8 and 9). Such clearly depicted lines of descent precipitated vibrant waves of systematic study using successively more sophisticated methods and information bases for judging relationship and inferring phylogenies.

appealed to Guy's preference for personal accountability for one's ideas and control (more or less) over content and secured his involvement in our next joint ventures with the superfamily (78, 103). In preparing the 1993 chapter and especially its 2005 successor, we were staggered by the voluminous literature that had appeared since Honacki et al. (1982), particularly because many specific and generic accounts were informed not simply by literature compilation but also through specimen examination, insofar as possible (availability of specimens) or practical (availability of time). For example, the specific and generic accounts of African murines and assorted "archaic" muroids were extensively upgraded, compared with contemporary standards (Misonne, 1974; Honacki et al., 1982; Corbet and Hill, 1991), based on inspection of the large African series in the AMNH and USNM, supplemented by trips to or loans from the

Field Museum of Natural History and Museum of Comparative Zoology, and nomenclaturally grounded on Guy's prior studies of BMNH types. I thought that we had pushed the envelope on the amount of specimen examination in researching the 1993 edition, but museum documentation, as cited within distributions and comments, grew appreciably in the 2005 edition (as appreciated by Solari and Baker, 2007, in their review). As I reviewed Guy's first drafts of various murines, one reason for the difference became apparent: with retirement fast approaching, the third edition of MSW represented the last opportunity to record incidental results accumulated during his many years of specimen examination in European and Asian museums. Whereas the 1984 and 1993 muroid contributions were never intended to be formal family-group classifications, the six-family arrangement presented in the 2005 chapter was, and it broke with the recent classificatory habit to place all subfamilies under one huge Family Muridae (e.g, Corbet and Hill, 1991; Musser and Carleton, 1993 [78]; McKenna and Bell, 1997). The 2005 classification drew upon our 1984 synthesis of morphological and paleontological information (54), historically influential arrangements of the superfamily, and the fresh insight to those past classifications supplied by the rapidly proliferating, taxonomically broad molecular investigations (that of Michaux et al., 2001, was pivotal). During the years of composing the 1993 and 2005 contributions, a lively correspondence transpired, as much to bolster one another's sagging enthusiasm to persevere as to exchange ideas.

> Back to the list (last night I dreamed of sorting rats and typing entries). (GGM, in litt., 10 October 1991)

> The four species of *Petromyscus* are diagnosed by such clear qualitative and quantitative traits, and by geography and habitat, that someone should have sorted them out long ago instead of continuing the same old bad taxonomy in current lists... Back to Murinae—Argh! (GGM, in litt., 22 October 1991)

> Spent 3 days or more on *Mus musculus*, what a nightmare, but interesting... I think the Murinae may increase by as much as a third of the past edition, which will probably make [Don] Wilson see red. There is no way I can finish everything by January 1. (GGM, in litt., 6 December 2001)

> Just about to leave for home... Spent most of the day sorting out our [AMNH] *Eothenomys* specimens to be sure my accounts were accurate. (GGM, in litt., 7 February 2002)

> I dread the library these days—every new pertinent paper seems a chore. (GGM, in litt., 28 February 2002)

> That should clear up Arvicolinae. Let us hope that somebody does not publish anything else between now and when we submit it to Don [Wilson] and DeeAnn [Reeder]. I don't want to see any more vole literature. The next time I see a *Microtus pennsylvanicus* at the campground I will step on it. (GGM, in litt., 18 July 2002)

> I guess I am becoming cranky and disinterested in these problems as the last of the checklist nears completion [editors had extended the literature cutoff to 30 June]. I just want to get the damn thing done, but in the right way of course. (GGM, in litt., 24 March 2003)

Although my prejudice is justifiably suspect, I thought that we did it the "right way," or as right as one could achieve for Mammalia's richest clade, from the species to family ranks, with due attribution of the classic and recent literature on extant and extinct muroids, and constrained to the format of a "species checklist."

Research Approach: "Sorting" is a fundamental method mentioned in many of Guy's papers, usually in the context of defining the taxonomic problem, as in: "I have sorted the specimens into five lots, each defined and distinguished from the others by a combination of features... I judge that each lot represents a species" (Musser, 1979 [35]: 388); or, "Sorting and studying museum specimens... has allowed us to document the morphological and distributional limits of 10 Neotropical species" (Musser et al., 1998 [89]: 5). To sort, according to the sense intended here, is to "arrange systematically or according to type, class, etc.; separate and put into different sorts" (Oxford English Dictionary, II 6). The dictionary definition intimates that "types" and "classes" are somehow preexisting, that the activity is little more than a casual shuffling of specimens into already defined groups based on self-evident characteristics. To the contrary, sorting is an

investigational tool in its own right, an objective means to discern natural units of meaningful biological significance, or as the method was aptly characterized by Kohler (2006: 227): "The act of sorting and categorizing is as theoretically creative as any scientific act." In a storage cabinet in the UMMZ mammal range, Hooper maintained a stack of specimen examination boards, cut from eighth-inch masonite sheets into various rectangular sizes, from ca. 8 × 12 to 12 × 20 inches, and spray-painted a flat black to accentuate the osseous white of mammal skulls. Generic identifications of a new collections accession could be reliably ascertained based on features of the skin, but when specific determinations in problematic genera such as *Peromyscus* or *Reithrodontomys* were required, out came the examination boards. Skulls were first aligned by occipitonasal length, dorsal side up, to uncover possible assortment of gender with size and to judge interorbital configuration, zygomatic spread, and rostral proportion in relation to size. Skulls would then be flipped over, ventral side up, to appreciate possible correspondence of molar wear (age) to increasing size and to view conformation of incisive foramina, robustness of molar rows, and relative bullar inflation. Series of specimens of known species from nearby localities might be arrayed on the examination boards, together with the unknowns, and extensive comparisons, dorsal and ventral, would be repeated. This iterative routine, patiently and skillfully applied, was keenly sensitive to appraising subtle variational patterns in cranial size and shape and to disclosing specific gaps in those patterns. Sorting, as practiced by the best of our predecessors, was essentially a forerunner of multivariate factor analysis, minus the digital data, covariance matrices, and variable loading coefficients. Guy was—is—among the best, so it is little wonder that species and genera of the unrevised Indo-Australian murid fauna would, for him, "sort out like nuts and bolts" ("I still hear his [Hooper's] voice in my ear and feel his presence over my shoulder every time I lay out a string of skulls."—GGM, in litt., 2 August 1992). With the advent of molecular bar-coding as the first approximation of specific identification, sorting of specimens, like the "-ology" courses, may pass into obscurity.

The extended field sabbatical in Sulawesi (1973–1976), following years of studying specimens in museums, conforms to a recurring theme of Guy's systematic approach, the interplay of field versus museum perspectives and the reciprocal illumination that each brings to the other. A tropical forest can be bewildering to comprehend, with its infinite variety and immense complexity, but a rodent caught in a trap deliberately placed by the investigator supplies a concrete bit of information—the first hypothesis tested. The requisite next question to ask is what scientific name should be applied to the specimen, an antithetical hypothesis elaborated through recourse to the comparative material and type specimens contained in the world's museums. Guy variously highlighted the contrapuntal theses of forest and museum in conveying his taxonomic conclusions, such as: "My experiences in the forests of Celebes gave reality to a picture that I had formed while I was working in museums" (Musser, 1977 [33]: 1); or, "Our report represents only a beginning, an understanding in the museum of the first lesson in the forest" (Musser et al., 1998 [89]: 324). The length of Guy's fieldwork in Sulawesi, three years, also underscores key aspects of his work habits: a drive to get it right and pertinacity to resolve as many taxonomic questions as possible, without regard to the practical time constraints that truncate the research aspirations of most of us. Guy is relentlessly methodical and thorough, which are useful compulsions for good scientific research in general, but his uncompromising adherence to these qualities is exceptional and surpassed by few other mammalogists in my experience. His papers decidedly evince a preference for working at a tangible empirical level and eschew abstract theorizing. He does not dither over species concepts from paper to paper; instead his specific descriptions and amendments are abundantly accompanied by enumeration and illustration of differentiating traits. Primary source materials, vouchered specimens and the distributional data associated with them, form the core of his taxonomic studies and anchor any commentary on biogeography and phylogeny.

The diagnostic traits of a Musser publication—replete historical and biological context, detailed morphological description, exhaustive taxonomic comparison, and elegant illustration—coalesced during Guy's second phase of murine publications (1979–1987). The AMNH has always liberally supported the illustrational needs of its scientists, and Guy just as liberally availed himself of those artistic talents and funds. He has an artful knack for judging the illustrational needs required to tell a paper's story. Assembling the figures, maps, and tables is, for him, just as critical to communicating results of one's study as is composing the text ("I really see the need to have illustrations and a simple diagram of terms. I can picture the tooth in my head but readers will have a tough time."—GGM, in litt., 12 December 1988). Although some may find the description overmuch and the illustration excessive, Guy's reason for this approach is difficult to assail: to consolidate at one time and place the involved nomenclatural histories, empirical specimen-based data scattered amongst the world's museums, and all character information on which his own taxonomic results are based. An overarching motivation has been to spare future systematists the time and effort that he was forced to expend in trying to comprehend the taxonomic pronouncements of his predecessors. He reflected on these points as an aside when reviewing one of my papers.

> There are probably some persons who would have you cut the paper in half but that would necessitate removing the analyses of the data and thus would not allow readers to know how you arrived at your conclusions.... I have faced this problem from the time I began to write about rats and mice of the Far East. Faced with a mountain of dogmatic literature based on opinions and with no hard data, I have had to carefully document every damn change in the taxonomy of murids. The process results in longer papers that have to be put into context.... Readers know what questions I am asking and why they are important and can see the data for themselves and the reasons I formed my conclusions. (GGM, in litt., 27 May 1978)

His words may sound like banal truisms measured by today's standards of systematic research (though not always the practice). However, the quotation must be understood from the perspective of a new Archbold Assistant Curator, grappling with a daunting body of systematic literature set forth by luminaries such as Thomas, Miller, and Ellerman, and judged against the meagre documentation that accompanied the far-reaching biogeographic and phylogenetic implications of their specific and generic taxonomies.

A Museum Conscience That Joseph Grinnell Would Approve

Chairman and Collection Duties: When Guy joined the AMNH Department of Mammalogy in 1966, his responsibility was mostly confined to research, as departmental roles were delineated by Van Gelder. Promotions to Archbold Associate Curator (1970) and Archbold Curator (1976) followed mainly in recognition of his research output and extensive fieldwork. Guy was early on immersed in collections curation, although such activities were then related to his immediate research projects—foremost Indo-Australian murids of the Archbold collections, to a lesser degree the extensive holdings of South American cricetids acquired by Anthony and Tate in the early 1900s. Inside-the-case experiences with the latter gave Guy a sobering glimse of the curatorial needs of the department as a whole.

> Well, this gives you some idea of the curatorial headache we have with the South American cricetines [Sigmodontinae]. A lot of real good stuff, but much has never been identified—literally whole cabinents full. And the fluid-preserved material is another whole mess. (GGM, in litt., 1 November 1972)

Guy became chairman of the department in 1981, following the terms of Van Gelder (1959–1974) and Anderson (1975–1981), and launched a long (1981–1993), concerted program to upgrade the physical storage and curatorial order of the entire mammal holdings, which had been sadly neglected for decades. Guy was successful in securing several NSF collection support grants (1981–1990), which allowed purchase of new cases for decompression of overcrowded cases and wholesale reorganization of large, heavily

utilized orders, such as marsupials, carnivores, and primates. The dust-covered, unidentified jars of fluid specimens were removed from the back stairwells and arranged taxonomically within a new alcohol range that featured compactor shelving. Ungulate skeletons scattered throughout attics and other wings of the museum were consolidated and recurated to become again accessible to visitors. Storage and arrangement of large, tanned skins were improved. Attention was also devoted to upgrading the physical plant, including plastering and painting of the ranges and offices and the installation of air conditioners to exclude the dust and soot that permeated the collections when windows were opened during the summer months. Guy's involvement in these improvements included supervisory oversight as well as much hands-on curation, verifying identifications so that groups could be properly rearranged into new trays and cases. At the halfway point of his chairmanship, Guy assessed the status of the collections as follows.

> I am trying to finish departmental work just in case [the Director ends my appointment as Chair]. This means working on our archives (library, records, and other items), curating the carnivores and marsupials, and other odd jobs. I am getting a little tired of shifting cases and scrounging for this and that, and recurating; six years of this has worn all of us out but there is more to be done. And I thought we could finish everything in two years or so. Turns out none of us had any idea of the magnitude of the lousy shape parts of the collection were in. There are still years worth of minor recuration but at least the big tasks will be done. (GGM, in litt., 12 October 1987)

The curatorial achievements owed much to a dedicated support staff, in particular Helmut Sommer, who long worked (1959–1997) as technician in the Mammalogy Department. Rescued from the museum's defunct taxidermic unit, Helmut was delighted and inspired to see the multifaceted attention being devoted to the mammal collections after Guy became chairman. The two developed an effective working bond and collaborated to correct specimen identifications uncovered during Helmut's curation of marsupials (72). Guy considered him to be a museum-based member of the Archbold Sulawesi Expedition and acknowledged his reliance on Helmut's wide-ranging capabilities in naming a new genus of Sulawesi rodent (*Sommeromys* Musser and Durden, 2002). Another focus of recuration was the type collection, along with revision of the type catalog, which projects Guy entrusted to Marie Lawrence. The two amended a taxonomic oversight discovered during Marie's curation (66), and after her unexpected death in 1992, Guy assumed the final editing chores that brought her first draft of the type catalog to publishable form (Lawrence, 1993). Any long-term user of the AMNH mammal collections readily appreciates the many and vast improvements he effected during his tenure as chairman.

Hooper was a student of Grinnell and reverently absorbed his professor's short commentary (1922) on "The Museum Conscience." Hooper observed Grinnell's dual essentials of a scientific museum—order and accuracy—in his assiduous care and curation of the UMMZ mammal collection, standards of excellence that were surely impressed upon Guy during his graduate years at Michigan. In closing his essay, Grinnell (1922: 63) remarked that "My visits to the larger museums have left me with the unpleasant and very distinct conviction that a large portion of the vertebrate collections in this country... are in far from satisfactory condition with respect to the matters here emphasized." Reading between the lines, it seems probable that his remarks on "larger museums" were directed, in part, at the AMNH and USNM. That a second-generation, academic descendent of Grinnell would begin to redress unsatisfactory conditions of the AMNH mammal collection was somehow fitting.

In spite of the substantial progress in collection improvement, Guy considered that his most important accomplishment as chair was to give Karl Koopman free rein to concentrate soley on his bat research. Under previous chairs, Karl was the curatorial specialist of Chiroptera, which, in addition to research, involved such tasks as pulling specimens for loans and answering information requests. Among the curators in the Mammalogy Department when Guy arrived, he and Karl developed a special friendship although they seldom collaborated on scien-

tific matters (49, 83). Guy twice acknowledged Karl's intellectual breadth and contributions to systematic biology in describing new murine species (*Chiropodomys karlkoopmani* Musser 1979; *Rattus koopmani* Musser and Holden 1991) and regularly sought his input as reviewer of presubmission drafts. When Karl started to mutter about the unseemly increase of murid genera and species, Guy would thereafter present a manuscript along with a tray of rat skins and skulls so that Karl could verify the traits mentioned in diagnoses and comparisons. The muttering stopped.

OTHER PROFESSIONAL ACTIVITIES AND HONORS: Guy has had little formal involvement in academia and the matriculation of future mammalogists, partly given his position in an independent museum and partly due to his conviction that research and curation in a huge collection are by themselves fulltime endeavors. Nevertheless, Guy has influenced many graduate students through his curatorial efforts to make the AMNH mammal collections accessible for their research, sponsorship of short-term visitor awards, and encouragement of collection internships under which graduate students could simultaneously conduct their own specimen examinations and recurate a portion of the mammal collection. He regularly participated in the Susan Greenwall Foundation, administered by the AMNH, and involved graduate students as collaborators in his own research projects (52, 56, 59, 61). Guy has shown especial willingness to review the manuscripts of graduate students or younger colleagues and has volunteered detailed and thoughtful, sometimes hard-nosed but always constructive, advice on how to write a systematic paper, frame a species description, or develop a taxonomic revision ("You need more illustrations!" was a familiar urging). In this informal capacity, his involvement in the education of systematic mammalogists has been generous and substantial, benefiting the professional development of most contributors to this volume among many others.

Guy's professional activities in the American Society of Mammalogists (ASM) included turns as editor for General Notes (1971) and editor for Feature Articles (1972–1973) for the society's journal and membership on various standing committees (Bibliography Committee, 1978–1980, which compiled the now-discontinued Recent Literature sections of the journal; Nomenclature Committee, 1978–1982; and the Checklist Committee, 1983–present, essentially responsible for producing revised editions of *Mammal Species of the World*). Guy is by nature a private individual, tends to shun gregarious settings like scientific meetings, and is uninterested in the prestige of holding societal offices. Given the usual constraints of budgets and time, he has preferred writing papers over giving talks, visiting museums over attending meetings. Notwithstanding his infrequent attendance at annual meetings, the ASM has bestowed two of its highest honors upon Guy. In 1992, he received the C. Hart Merriam Award, established primarily to give recognition to mammalogists with a stellar record in scientific research and singling out "his seminal contributions to understanding the systematics of murid rodents and because he is internationally recognized as an outstanding systematist." In 2004, two years into retirement, he was elected to honorary membership in the ASM, an esteemed honor bequeathed for a distinguished record of achievement in the science of mammalogy.

Several mammalian species have been named to honor Guy, including a shrew (*Crocidura musseri* Ruedi, 1995) and, naturally, several species of muroid rodents (*Microhydromys musseri* Flannery, 1989; *Archboldomys musseri* Rickart, Heaney, Tabaranza, and Balete, 1998; *Neacomys musseri* Patton, da Silva, and Malcolm, 2000; *Coryphomys musseri* Aplin and Helgen, in press). A surprising number of invertebrate patronyms have been named, reflecting Guy's encouragement of such researchers to use the Sulawesian collections and glean parasites (fleas—*Neopsylla musseri* Beaucournu and Durden 1999; a suckling louse—*Hoplopleura musseri* Durden 1990; a fur mite—*Listrophoroides musseri* Bochkov and OConnor 2005; and a nematode—*Heligmonoides musseri* Hasegawa and Syafruddin 1994); the collegiality formed with one of those specialists, Lance A. Durden, led to their fruitful collaborations on suckling ice of Murinae (70, 73, 80, 81, 93). The present volume

appropriately continues this honorific mode: *Crocidura guy* Jenkins, Lunde, and Moncrieff; *Reithrodontomys musseri* Gardner and Carleton; and *Musseromys* Heaney, Balete, Rickart, Veluz, and Jansa.

Curator Emeritus (2002–present)

> Adjusting to retirement away from the museum has taken more time than anticipated. There are still days when I get the knee-jerk reaction to commute into the museum. On the other hand, once I left the building...I felt liberated. However, the pressure and stress to keep working on research projects is greater than it was during my employment. It was certainly time to leave and I have no regrets. (GGM, in litt., 11 December 2002)

Guy retired from the AMNH on 11 September 2002, and he, his spouse Mary Ellen (Holden, herself a systematic mammalogist and occasional collaborator), and family of three moved to South Carolina in November, to be nearer her family and the children nearer to their grandparents. Although formally retired, he has managed a very active research program (fig. 1, appendix 1), in spite of the isolation from a world-class scientific library and immense museum collection. At the time of his retirement, he was mired in the composition of chapters for *Mammal Species of the World* (101–103), which were not completed until he had relocated to South Carolina. Thanks to the internet, he has maintained collaborative projects and continued his studies on Sulawesi murines (100, 104, 106, 108; and others in preparation), Sulawesi squirrels (in preparation, with L.A. Durden), and oryzomyines (107). In view of Guy's ongoing projects, this scientific biography is necessarily incomplete and must end abruptly.

> Yesterday I abandoned SCIENCE and FAMILY and escaped to the tidal creeks to catch red drum and watch kingfishers dive, white ibis stand nearby, and little blue herons mess around. Since I am supposed to be retired, I can act irresponsible sometimes. (GGM, in litt., 19 November 2003)

The participants in this festschrift, and undoubtedly others who have known Guy personally or professionally through his research, will happily excuse such occasional flights of irresponsibility and heartily wish him more of them. His internal sense of responsibility may not be so approving.

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I count myself privileged to have coauthored several publications with Guy, and in a sense, this biographical sketch is yet another collaboration as I have attempted to interweave a first-person perspective throughout the text. For this former UMMZ student, Guy's encouragement to publish my results and timely advice offered along the way proved pivotal in orienting my mammalogical career. Over the years, he has functioned as a senior graduate student counselor, à la M. Raymond Lee, an unofficial adjunct committee member, professional colleague, and friend.

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Tate, G.G.H., and R. Archbold. 1935. Results of the Archbold Expeditions. No. 2. Twelve apparently new forms of *Rattus* from the Indo-Australian region. American Museum Novitates 802: 1–10.

Voss, R.S. 1988. Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. Bulletin of the American Museum of Natural History 188 (2): 259–493.

Voss, R.S., and A.V. Linzey. 1981. Comparative gross morphology of male accessory glands among Neotropical Muridae (Mammalia: Rodentia) with comments on systematic implications. Miscellaneous Publications Museum of Zoology, University of Michigan 159: 1–41.

Weksler, M. 2006. Phylogenetic relationships of oryzomine rodents (Muroidea: Sigmodontinae): separate and combined analyses of morphological and molecular data. Bulletin of the American Museum of Natural History 296: 1–149.

Weksler, M., A.R. Percequillo, and R.S. Voss. 2006. Ten new genera of oryzomyine rodents (Cricetidae: Sigmodontinae). American Museum Novitates 3537: 1–29.

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Wilson, D.E. and D.M. Reeder (editors). 2005. Mammal species of the world: a taxonomic and geographic reference. 3rd ed. Baltimore, MD: Johns Hopkins University Press, Vols. 1 (xxxv + 1–744) and 2 (xvii + 745–2142).

APPENDIX 1

Scientific Publications of Guy G. Musser

(Arranged by year to accentuate the pace and evolving research focus of his publications; this data formed the basis for the graphical summary in fig. 1. Numbers at the left-hand margin correspond to those used in the text to reference Musser's publications.)

1. Edmunds, G.F., and G.G. Musser. 1960. The mayfly fauna of Green River in the Flaming Gorge Reservoir Basin, Wyoming and Utah. *In* Angus Woodbury et al. (eds.), "Ecological studies of the flora and fauna of Flaming Gorge Reservoir Basin, Utah and Wyoming." University of Utah Anthropology papers, No. 48, Upper Colorado Series, No. 3: 125–131.
2. Musser, G.G., and S.D. Durrant. 1960. Notes on *Myotis thysanodes* in Utah. Journal of Mammalogy 41: 393–394.
3. Musser, G.G. 1961. A new subspecies of flying squirrel (*Glaucomys sabrinus*) from southwestern Utah. Proceedings of the Biological Society of Washington 74: 119–126.
4. Hooper, E.T., and G.G. Musser. 1964. The glans penis in Neotropical cricetines (Family Muridae), with comments on classification of muroid rodents. Miscellaneous Publications Museum of Zoology, University of Michigan 124: 1–57.
5. Hooper, E.T., and G.G. Musser. 1964. Notes on classification of the rodent genus *Peromyscus*. Occasional Papers Museum of Zoology, University of Michigan 635: 1–13.
6. Musser, G.G. 1964. Notes on geographic distribution, habitat, and taxonomy of some Mexican mammals. Occasional Papers Museum of Zoology, University of Michigan 636: 1–22.
7. Musser, G.G., and V.H. Shoemaker. 1965. Oxygen consumption and body temperature in relation to ambient temperature in the Mexican deer mice, *Peromyscus thomasi* and *P. megalops*. Occasional Papers Museum of Zoology, University of Michigan 643: 1–15.
8. Hooper, E.T., and G.G. Musser. 1966. Bibliography: Mammals. BioScience 16: 291–292.
9. Musser, G.G. 1968. A systematic study of the Mexican and Guatemalan gray squirrel *Sciurus aureogaster*, F. Cuvier (Rodentia, Sciuridae). Miscellaneous Publications Museum of Zoology, University of Michigan 137: 1–112.
10. Musser, G.G. 1969. Notes on *Peromyscus* (Muridae) of Mexico and Central America. American Museum Novitates 2357: 1–23.
11. Musser, G.G. 1969. Results of the Archbold Expeditions. No. 89. Notes on the taxonomic status of *Rattus aspinatus* Tate and Archbold, and *Mus callitrichus* Jentink (Rodentia, Muridae). American Museum Novitates 2365: 1–9.
12. Musser, G.G. 1969. Results of the Archbold Expeditions. No. 91. A new genus and species of murid rodent from Celebes, with a discussion of its relationships. American Museum Novitates 2384: 1–41.
13. Musser, G.G. 1969 Results of the Archbold Expeditions. No. 92. Taxonomic notes on *Rattus dollmani* and *R. hellwaldi* (Rodentia, Muridae) of Celebes. American Museum Novitates 2386: 1–24.
14. Musser, G.G. 1969. [Review of] Biology of *Peromyscus* (Rodentia), edited by John A. King. Journal of Mammalogy 50: 655–657.
15. Musser, G.G. 1970. Species limits of *Rattus brahma*, a murid rodent of northeastern India and northern Burma. American Museum Novitates 2406: 1–27.
16. Musser, G.G. 1970. Identity of the type-specimens of *Sciurus aureogaster* F. Cuvier and *Sciurus nigrescens* Bennett (Mammalia, Sciuridae). American Museum Novitates 2438: 1–19.
17. Musser, G.G. 1970. Results of the Archbold Expeditions. No. 93. Reidentification and reallocation of *Mus callitrichus* and allocations of *Rattus maculipilis*, *R. m. jentinki*, and *R. microbullatus* (Rodentia, Muridae). American Museum Novitates 2440: 1–35.
18. Musser, G.G. 1970. *Rattus masaretes*: A synonym of *Rattus rattus mollucarius*. Journal of Mammalogy 51: 606–609.
19. Musser, G.G. 1970. The taxonomic identity of *Mus bocourti* A. Milne Edwards (1874) (Mammalia: Muridae). Mammalia 34: 484–490.
20. Musser, G.G. 1971. *Peromyscus allophylus* Osgood: A synonym of *Peromyscus gymnotis* Thomas (Rodentia, Muridae). American Museum Novitates 2453: 1–10.
21. Musser, G.G. 1971. Results of the Archbold Expeditions. No. 94. Taxonomic status of *Rattus tatei* and *Rattus frosti*, two taxa of murid rodents known from middle Celebes. American Museum Novitates 2454: 1–19.
22. Musser, G.G. 1971. The taxonomic status of *Rattus dammermani* Thomas and *Rattus toxi* Sody (Rodentia, Muridae) of Celebes. Beaufortia 18 (242): 205–216.
23. Musser, G.G. 1971. The taxonomic association of *Mus faberi* Jentink with *Rattus xanthurus* (Gray), a species known only from Celebes (Rodentia: Muridae). Zoologische Mededelingen, Rijksmuseum van Natuurlijke Historie, Leiden 45: 107–118.
24. Musser, G.G. 1971. The identities and allocations of *Taeromys paraxanthus* and *T. tatei*, two taxa based on composite holotypes (Rodentia, Muridae). Zoologische Mededelingen, Rijksmuseum van Natuurlijke Historie, Leiden 45: 127–138.
25. Musser, G.G. 1971. The taxonomic status of *Rattus tondanus* Sody and notes on the holotypes of *R. beccarii* (Jentink) and *R. thysanurus* Sody (Rodentia: Muridae). Zoologische Medelingen, Rijksmuseum van Natuurlijke Historie, Leiden 45: 147–157.
26. Musser, G.G. 1972. The species of *Hapalomys* (Rodentia, Muridae). American Museum Novitates 2503: 1–27.
27. Musser, G.G. 1972. Identities of taxa associated with *Rattus rattus* (Rodentia, Muridae) of Sumba Island, Indonesia. Journal of Mammalogy 53: 861–865.

28. Musser, G.G. 1973. Zoogeographical significance of the ricefield rat, *Rattus argentiventer*, on Celebes and New Guinea and the identity of *Rattus pesticulus*. American Museum Novitates 2511: 1–30.
29. Musser, G.G. 1973. Species-limits of *Rattus cremoriventer* and *Rattus langbianis*, murid rodents of Southeast Asia and the Greater Sunda Islands. American Museum Novitates 2525: 1–65.
30. Musser, G.G. 1973. Notes on additional specimens of *Rattus brahma*. Journal of Mammalogy 54: 267–270.
31. Musser, G.G., and A.L. Gardner. 1974. A new species of the ichthyomyine *Daptomys* from Perú. American Museum Novitates 2537: 1–23.
32. Robertson, P.B., and G.G. Musser. 1976. A new species of *Peromyscus* (Rodentia: Cricetidae), and a new specimen of *P. simulatus* from southern Mexico with comments on their ecology. Occasional Papers of the Museum of Natural History, The University of Kansas 47: 1–8.
33. Musser, G.G. 1977. *Epimys benguetensis*, a composite, and one zoogeographic view of rat and mouse faunas in the Philippines and Celebes. American Museum Novitates 2624: 1–15.
34. Musser, G.G. 1977. Results of the Archbold Expeditions. No. 100. Notes on the Philippine rat, *Limnomys*, and the identity of *Limnomys picinus*, a composite. American Museum Novitates 2636: 1–14.
35. Musser, G.G. 1979. Results of the Archbold Expeditions. No. 102. The species of *Chiropodomys*, arboreal mice of Indochina and the Malay Archipelago. Bulletin of the American Museum Natural History 162: 377–445.
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37. Musser, G.G., J. T. Marshall, Jr., and Boeadi. 1979. Definition and contents of the Sundaic genus *Maxomys* (Rodentia, Muridae). Journal of Mammalogy 60: 592–606.
38. Musser, G.G., and Boeadi. 1980. A new genus of murid rodent from the Komodo Islands in Nusatenggara, Indonesia. Journal of Mammalogy 61: 395–413.
39. Musser, G.G. 1981. Results of the Archbold Expeditions. No. 105. Notes on systematics of Indo-Malayan murid rodents, and descriptions of new genera and species from Ceylon, Sulawesi, and the Philippines. Bulletin of the American Museum of Natural History 168: 225–334.
40. Musser, G.G. 1981. The giant rat of Flores and its relatives east of Borneo and Bali. Bulletin of the American Museum of Natural History 169: 67–176.
41. Musser, G.G. 1981. A new genus of arboreal rat from West Java, Indonesia. Zoologische Verhandelingen, Rijksmuseum van Natuurlijke Historie, Leiden 189: 1–40.
42. Musser, G.G., and P.W. Freeman. 1981. A new species of *Rhynchomys* (Muridae) from the Philippines. Journal of Mammalogy 62: 154–159.
43. Musser, G.G., and L.K. Gordon. 1981. A new species of *Crateromys* (Muridae) from the Philippines. Journal of Mammalogy 62: 513–525.
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45. Musser, G.G. 1982. Results of the Archbold Expeditions. No. 107. A new genus of arboreal rat from Luzon Island in the Philippines. American Museum Novitates 2730: 1–23.
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47. Musser, G.G. 1982. Results of the Archbold Expeditions. No. 110. *Crunomys* and the small-bodied shrew rats native to the Philippine Islands and Sulawesi (Celebes). Bulletin of the American Museum of Natural History 174: 1–95.
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55. Musser, G.G., and M.M. Williams. 1985. Systematic studies of oryzomyine rodents (Muridae): definitions of *Oryzomys villosus* and *Oryzomys talamancae*. American Museum Novitates 2810: 1–22.
56. Musser, G.G., and C. Newcomb. 1985. Definitions of Indochinese *Rattus losea* and a new species from Vietnam. American Museum Novitates 2814: 1–32.
57. Musser, G.G., and L.R. Heaney. 1985. Philippine *Rattus*: a new species from the Sulu Archipelago. American Museum Novitates 2818: 1–32.
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60. Musser, G.G. 1986. Sundaic *Rattus*: definitions of *Rattus baluensis* and *Rattus korinchi*. American Museum Novitates 2862: 1–24.
61. Musser, G.G., and M. Dagosto. 1987. The identity of *Tarsius pumilus*, a pygmy species endemic to the montane mossy forests of central Sulawesi. American Museum Novitates 2867: 1–53.
62. Musser, G.G. 1987. The occurrence of *Hadromys* (Rodentia: Muridae) in Early Pleistocene Siwalik strata in northern Pakistan and its bearing on biogeograhic affinities between Indian and northeastern African murine faunas. American Museum Novitates 2883: 1–36.
63. Musser, G.G. 1987. The mammals of Sulawesi. *In* T.C. Whitmore (ed.), Biogeographic evolution of the Malay Archipelago: 73–93. Oxford: Oxford University Press, 147 pp.
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65. Carleton, M.D., and G.G. Musser. 1989. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): a synopsis of *Microryzomys*. Bulletin of the American Museum of Natural History 191: 1–83.
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68. Musser, G.G. 1991. Sulawesi rodents (Muridae, Murinae): descriptions of new species of *Bunomys* and *Maxomys*. American Museum Novitates 3001: 1–41.
69. Breed, W.G., and G.G. Musser. 1991. Sulawesi and Philippine rodents (Muridae): a survey of spermatozoal morphology and its significance for phylogenetic inference. American Museum Novitates 3003: 1–15.
70. Durden, L.A., and G.G. Musser. 1991. A new species of sucking louse (Insecta, Anoplura) from a montane forest rat in Central Sulawesi and a preliminary interpretation of the sucking louse fauna of Sulawesi. American Museum Novitates 3008: 1–10.
71. Musser, G.G., and M.E. Holden. 1991. Sulawesi rodents (Muridae, Murinae): morphological and geographical boundaries of species in the *Rattus hoffmanni* Group and a new species from Pulau Peleng. *In* T.A. Griffiths and D. Klingener (eds.), Contributions to mammalogy in honor of Karl F. Koopman: 322–413. Bulletin of the American Museum of Natural History, 206: 432 pp.
72. Musser, G.G., and H.G. Sommer. 1992. Taxonomic notes on specimens of the marsupials *Pseudocheirus schlegelii* and *P. forbesi* (Diprotodontia, Pseudocheiridae) in the American Museum of Natural History. American Museum Novitates 3044: 1–16.
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75. Rickart, E.A, and G.G. Musser. 1993. Philippine rodents: chromosomal characteristics and their significance for phylogenetic inference among 13 species (Rodentia: Muridae: Murinae). American Museum Novitates 3064: 1–34.
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79. Musser, G.G., and E.M. Brothers. 1994. Identification of bandicoot rats from Thailand (*Bandicota*, Muridae, Rodentia). American Museum Novitates 3110: 1–56.
80. Durden, L.A., and G.G. Musser. 1994. The sucking lice (Insecta, Anoplura) of the world: a taxonomic checklist with records of mammalian hosts and their geographical distributions. Bulletin of the American Museum of Natural History 218: 1–90.
81. Durden, L.A., and G.G. Musser. 1994. The mammalian hosts of the sucking lice (Anoplura) of the world: a host-parasite list. Bulletin of the Society of Vector Ecology 19: 130–168.
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ridae: Sigmodontinae): definition and distribution of *Oligoryzomys vegetus* (Bangs, 1902). Proceedings of the Biological Society of Washington 108: 338–369.

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91. van der Meulen, A.J., and G.G. Musser. 1999. New paleontological data from the continental Plio-Pleistocene of Java. *In* J.W.F. Reumer and J. de Vos (eds.), Elephants have a snorkel! Papers in honour of Paul Y. Sondaar. Deinsea, 361–368.
92. Norris, C., and G.G. Musser. 2001. Systematic revision within the *Phalanger orientalis* complex (Marsupialia, Phalangeridae): a third species of lowland gray cuscus from New Guinea and Australia. American Museum Novitates 3356: 1–20.
93. Musser, G.G., and L.A. Durden. 2002. Sulawesi rodents (Muridae, Murinae): description of a new genus and species and its parasitic new species of sucking louse (Insecta, Anoplura). American Museum Novitates 3368: 1–50.
94. Lunde, D.P., and G.G. Musser. 2002. The capture of the Himalayan water shrew (*Chimarrogle himalayica*) in Vietnam. Mammal Study 27: 137–140.
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105. Lunde, D.P., N.T. Son, and G.G. Musser. 2007. A survey of small mammals from Huu Lien Nature Reserve, Lang Son Province, Vietnam. Mammal Study 32: 155–168.
106. Musser, G.G., K.M. Helgen, and D.P. Lunde. 2008. Systematic review of New Guinea *Leptomys* (Muridae: Murinae) with descriptions of two new species. American Museum Novitates 3624: 1–60.
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Chapter 2

Taxonomy, Distribution, and Natural History of the Genus *Heteromys* (Rodentia: Heteromyidae) in Central and Eastern Venezuela, with the Description of a New Species from the Cordillera de la Costa

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ABSTRACT

Heteromys anomalus is widely distributed along the Caribbean coast of South America and had been considered the only spiny pocket mouse present in Venezuela for several decades. Recent taxonomic studies in western Venezuela, however, have documented the presence of *H. australis* from the Cordillera de Mérida and described *H. oasicus* from the Península de Paraguaná. Here, we revise the genus *Heteromys* in central and eastern Venezuela as well as in Trinidad and Tobago. Morphological comparisons with samples of *H. anomalus* from throughout its known range in Venezuela and with representatives of all other recognized species of the genus indicate the existence of a species new to science, which we describe as *Heteromys catopterius* (the Overlook Spiny Pocket Mouse). This species ranges from 350 to 2425 m in elevation in the Cordillera de la Costa in northern Venezuela, with the vast majority of records above ca. 700 m. In central and eastern Venezuela, *H. anomalus* is found in the surrounding lowlands and lower slopes of the Cordillera. Externally, *H. catopterius* is darker than *H. anomalus* and lacks the distinctly rounded ears of that species. The new species averages larger than *H. anomalus* for most external and cranial measurements. Cranially, the two species have differences in proportion; the skulls of *H. catopterius* are proportionately wider (less elongated) than those of *H. anomalus*, with a relatively wider interorbital constriction, wider interparietal, and more inflated braincase. *Heteromys catopterius* occurs in wet montane forests (especially cloud forests) in four highland areas of the Cordillera de la Costa: the main Aragua-Carabobo chain, the El Ávila massif, the Serranía del Interior, and the Macizo Oriental. Presumably, the warm, dry lowlands of the Depresión de Unare represent a barrier for the species, separating populations in the Macizo Oriental from the more westerly populations. Large areas of the known ranges of both *H. catopterius* and *H. anomalus* are protected in the Venezuelan network of protected areas.

INTRODUCTION

The rodent family Heteromyidae is endemic to North and South America and includes three subfamilies: Dipodomyinae (kangaroo rats and kangaroo mice), Perognathinae (pocket mice, both silky and coarse haired), and Heteromyinae (spiny pocket mice; Wilson and Cole, 2000; Patton, 2005). Heteromyines represent a well-defined monophyletic group distinct from the two other living subfamilies (Hafner, 1981; Hafner and Hafner, 1983; Wahlert, 1991; Hafner et al., 2007; see also Ryan, 1989: 94–98; Brylski, 1990). Two extant genera, *Heteromys* and *Liomys*, are recognized in the Heteromyinae

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and can be distinguished from each other by a number of morphological characters (Williams et al., 1993; Anderson, 2003b; Patton, 2005; Anderson et al., 2006). Although phylogenetic analyses based on sequences of mitochondrial DNA indicate that *Liomys* is likely paraphyletic (and no synapomorphies for it are known), *Heteromys* has been recovered as monophyletic in studies using both morphological and genetic data (including several synapomorphies; Rogers and Vance, 2005; Anderson et al., 2006; Hafner et al., 2007). Some authors have suggested that all heteromyines should be placed in the genus *Heteromys* to avoid recognition of a paraphyletic *Liomys* (Hafner et al., 2007). However, we continue to recognize *Liomys* (sensu Williams et al., 1993; Patton, 2005) until conclusive studies with multiple independent data sources (e.g., unlinked nuclear markers) can be completed, allowing for a comprehensive reevaluation of the generic-level taxonomy of the subfamily (see Anderson et al., 2006: 1227)[3]. Species of *Liomys* inhabit deciduous forests and other semiarid tropical and subtropical habitats from southern Texas and northern Mexico to Panama (Genoways, 1973; Morales and Engstrom, 1989; Rogers and Engstrom, 1992; Williams et al., 1993), and species of *Heteromys* occur in relatively wet (typically evergreen) forests from southern Mexico to western Ecuador (Williams et al., 1993; Anderson, 1999, 2003b; Anderson and Jarrín-V., 2002). Whereas most species of heteromyids inhabit western North America, *Heteromys* is the only genus of the family to have colonized South America.

Present taxonomy recognizes nine species of *Heteromys*, including three that have been described recently (Williams et al., 1993; Anderson and Jarrín-V., 2002; Anderson, 2003b; Patton, 2005; Anderson and Timm, 2006). *Heteromys desmarestianus*, *H. gaumeri*, *H. nelsoni*, *H. nubicolens*, and *H. oresterus* are restricted to Central America and Mexico (but see Anderson, 1999, for one marginal locality of *H. desmarestianus* in extreme northwestern Colombia). In addition, two species are known to have extensive distributions in northwestern South America, and three others have restricted distributions there. For several decades, the widespread *H. anomalus* and *H. australis* were the only two species recognized for the main body of South America, with a marginal distribution indicated for *H. desmarestianus* (Cabrera, 1961; Honacki et al., 1982; Patton, 1993). *Heteromys australis* inhabits very mesic evergreen forests in the lowlands of the Chocó in northwestern Ecuador, western Colombia, and eastern Panama, as well as throughout much of the Colombian Andes up to ca. 2500 m in elevation (Anderson, 1999). An apparently disjunct population also exists in the Río Uribante drainage of the Cordillera de Mérida in western Venezuela (Anderson and Soriano, 1999; Anderson et al., 2002a). In contrast, *H. anomalus* inhabits both deciduous and evergreen tropical forests in northern South America, typically from near sea level up to ca. 1500–1600 m. It is distributed along the Caribbean coast of Colombia and Venezuela (including the Isla de Margarita) and in Trinidad and Tobago (Musso-Q., 1962; Anderson, 1999, 2003b; Anderson and Soriano, 1999), but not in Panama (Anderson, 1999; contra Rogers, 1990; Méndez, 1993;

[3] All recent phylogenetic studies of the Heteromyinae have recovered three monophyletic groups: (1) *Heteromys*; (2) *Liomys adspersus* and *L. salvini*; and (3) *L. irroratus*, *L. pictus*, and *L. spectabilis* (Rogers and Vance, 2005; Anderson et al., 2006; Hafner et al., 2007). The relationships among the three clades could not be resolved using morphological and allozymic data (Anderson et al., 2006). Analyses of DNA sequences from linked mitochondrial genes indicated that the *L. adspersus–L. salvini* clade occupies a basal position in the subfamily, sister to the remaining two clades (Rogers and Vance, 2005; Hafner et al., 2007). If this topology is corroborated by analyses of other independent datasets (e.g., sequences of multiple unlinked nuclear markers), generic-level taxonomy should be modified to reflect reconstructed evolutionary relationships in the group. Furthermore, given the substantial morphological, ecological, and genetic distinctiveness of the three clades (Genoways, 1973; Anderson et al., 2006), recognition of three genera would be warranted regardless of the relationships among the three clades (i.e., even if *Liomys*, as currently conceived, is not paraphyletic). An available name exists for the basal *adspersus–salvini* clade: *Schaeferia* (first described as a subgenus of *Liomys*, with type species *H. salvini*; von Lehmann and Schaefer, 1979: 232). Elevation of *Schaeferia* to full generic status, restriction of *Liomys* (with type species *H. alleni*, currently considered a synonym of *L. irroratus*) to members of the *irroratus–pictus–spectabilis* clade, and retention of current usage of *Heteromys* (with type species *Mus anomalus*) would provide valid genera for each of the monophyletic groups, acknowledge the substantial morphological and ecological distinctiveness of the three clades, and maximally preserve nomenclatural stability in the subfamily.

Williams et al., 1993; Nowak, 1999). The species is also known from parts of the dry upper Río Magdalena Valley in Colombia (Hernández-Camacho, 1956; Anderson, 1999, 2003b). In addition to these long-recognized taxa with large distributions, *H. teleus* was described recently from central-western Ecuador, where it inhabits highly seasonal evergreen forests (Anderson and Jarrín-V., 2002). Subsequently, *H. oasicus* was described from small areas of mesic vegetation on the Península de Paraguaná in northwestern Venezuela (Anderson, 2003b). Finally, a species of the *Heteromys desmarestianus* complex (provisionally referred to as *H. d. crassirostris*) has been confirmed for one locality in the Serranía del Darién in extreme northwestern Colombia, west of the Río Atrato–Río San Juan lowlands (= Bolívar Geosyncline; Hershkovitz, 1972); the species' distribution continues to the west in Panamá (Anderson, 1999; Anderson et al., 2006).

Here, we evaluate the taxonomic status of populations of *Heteromys* from central and eastern Venezuela, as well as Trinidad and Tobago. A previous study revised the genus in western Venezuela but noted the presence of an unrecognized species to the east and the need for taxonomic study of populations from that region (Anderson, 2003b: 24). In doing so, the current work completes the revision of the genus in the easternmost portion of its distribution (Venezuela and Trinidad and Tobago). Future work should reevaluate populations in central Colombia that may be specifically distinct from *H. australis* (Anderson, 1999: 620).

MATERIALS AND METHODS

Museum Specimens

We examined 1349 specimens of *Heteromys* from the principal study area of central and eastern Venezuela, as well as Trinidad and Tobago (appendix 1). Central and eastern Venezuela is here considered as the area east of the Río Yaracuy and the Río Cojedes (and its continuations, the Río Portuguesa and Río Apure). These rivers define the Depresión de Yaracuy (SAGCN, 1995; ≈ Depresión de Lara sensu Soriano et al., 1999), a lowland region that separates the Cordillera de Mérida (and Sierra de Aroa) from the Cordillera de la Costa (fig. 1). Material reported here from the principal study area (appendix 1) includes the overwhelming majority of specimens of *Heteromys* from that region available in museums in the United States and Venezuela, as well as critical historical material in the United Kingdom.

We also examined selected specimens from other regions (appendix 2). For statistical analyses, we took advantage of the several large series of *Heteromys* available from localities throughout northern Venezuela. We also examined representative samples of all currently recognized species of *Heteromys*, including all holotypes and lectotypes representing nominal taxa currently referred to the genus, with the exception of *H. desmarestianus psakastus*; in lieu of that holotype, we examined eight paratypes. Apparently, no holotype exists for *H. thompsonii*, a name that Lesson (1827) clearly used to refer to the spiny pocket mouse from Trinidad named by Thompson (1815) as *Mus anomalus*, now referred to as *H. anomalus*. We also report two specimens from western Venezuela that were not included in Anderson (2003b).

We examined external and cranial morphological characters, making comparisons among specimens of approximately the same age. Cranial nomenclature follows Wahlert (1985), Anderson and Timm (2006), and Anderson et al. (2006); see also Anderson (1999, 2003b) and Anderson and Jarrín-V. (2002). Specimens were assigned to the age classes of Rogers and Schmidly (1982) based on patterns of tooth eruption, toothwear, and molt. Age classes 1–3 represent juveniles and subadults, and classes 4–6 are progressively older adults. Age classes do not constitute a continuous variable (such as absolute age), but rather are categories roughly corresponding to relative age within population samples (Voss et al., 1990).

Localities and specimens examined from central and eastern Venezuela and from Trinidad and Tobago are detailed in the Gazetteer (appendix 1), and other specimens examined are listed separately (appendix 2). Specimens examined are housed in the

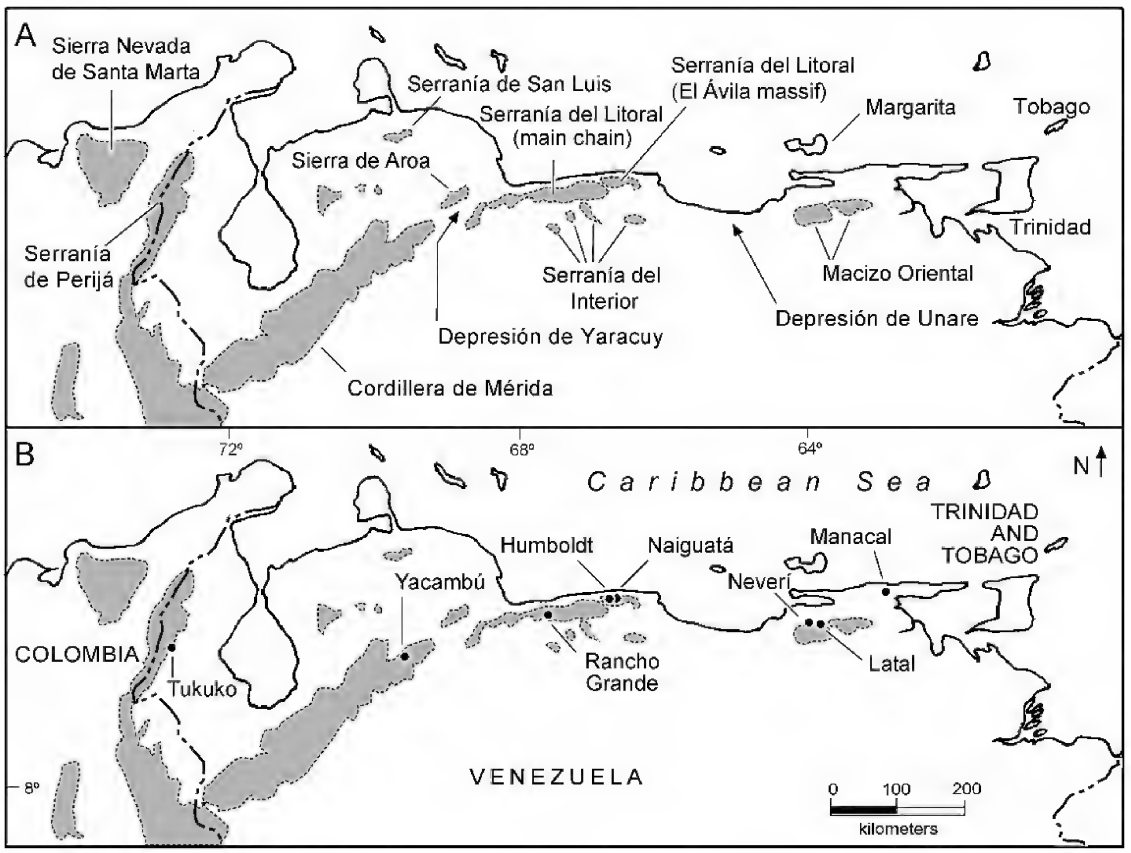

Fig. 1. Map of north-central South America. Gray shading approximates regions above 1000 m in elevation. **A** (upper): Major geographic features mentioned in the text. **B** (lower): Location of primary geographic samples of *Heteromys* used in this study. See Materials and Methods and appendices 1 and 2 for complete provenience and museum catalog numbers.

following museum collections (where applicable, abbreviations follow Lew and Ochoa, 1993; Bisbal-E. and Sánchez-H., 1997; and Hafner et al., 1997). An asterisk (*) denotes museums with material from central and eastern Venezuela or from Trinidad and Tobago.

AMNH	American Museum of Natural History, New York*
ANSP	Academy of Natural Sciences of Philadelphia, Philadelphia
BM(NH)	Natural History Museum, London [formerly British Museum (Natural History)]*
CM	Carnegie Museum of Natural History, Pittsburgh*
CUVC	Cornell University Vertebrate Collections, Ithaca*
CVULA	Colección de Vertebrados de la Universidad de los Andes, Mérida
EBRG	Museo de la Estación Biológica de Rancho Grande, Maracay*
FMNH	Field Museum, Chicago [formerly Field Museum of Natural History]*
ICN	Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá
KU	University of Kansas Natural History Museum, Lawrence*
MBUCV	Museo de Biología de la Universidad Central de Venezuela, Caracas*
MCNUSB	Museo de Ciencias Naturales de la Universidad Simón Bolívar, Caracas*

MCZ	Museum of Comparative Zoology, Harvard University, Cambridge*
MHNLS	Museo de Historia Natural La Salle, Caracas*
MIZA	Museo del Instituto de Zoología Agrícola de la Facultad de Agronomía de la Universidad Central de Venezuela, Maracay*
MNCR	Museo Nacional de Costa Rica, San José
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley
TCWC	Texas Cooperative Wildlife Collection, Texas A&M University, College Station*
TTU	Museum of Texas Tech University, Lubbock*
UF	Florida Museum of Natural History, University of Florida, Gainesville*
UMMZ	University of Michigan Museum of Zoology, Ann Arbor*
USNM	United States National Museum of Natural History, Washington, DC*
UV	Universidad del Valle, Cali*
UWZM	University of Wisconsin Zoological Museum, Madison*

Measurements

Standard cranial measurements for *Heteromys* (fig. 2) follow Anderson and Jarrín-V. (2002) and were taken to the nearest 0.01 mm with digital calipers on selected specimens (see below). External measurements and mass were copied from specimen tags and, when necessary, from primary field notes or museum catalogs. We calculated head-and-body length by subtracting tail length from total length.

Occipitonasal length (ONL): greatest distance from anteriormost projection of nasal bones to posteriormost portion of occipital bone.

Zygomatic breadth (ZB): greatest width across zygomatic arches at right angle to longitudinal axis of cranium.

Rostral length (RL): greatest distance from notch lateral to lacrimal bone to anteriormost projection of nasal bone on same side of cranium.

Nasal length (NL): greatest distance from anteriormost projection of one nasal bone to its posteriormost projection (not necessarily at medial suture between nasals).

Least interorbital constriction (IOC): least width across interorbital constriction at right angle to longitudinal axis of cranium.

Squamosal breadth (SB): width across squamosals anterior to external auditory meatus at right angle to longitudinal axis of cranium.

Maxillary toothrow length (MTR): distance from anterior lip of alveolus of premolar to posterior lip of alveolus of third molar.

Interparietal width (IW): greatest transverse width measured from lateralmost projections of interparietal bone at right angle to longitudinal axis of cranium.

Interparietal length (IL): greatest distance from anteriormost projection of interparietal bone to posteriormost border of interparietal bone, always taken along medial line of cranium even when notch present in posterior border.

Parietal breadth (PB): greatest width across parietal crests at right angle to longitudinal axis of cranium.

Skull depth (SD): greatest distance from dorsalmost point of braincase to horizontal plane passing through ventral borders of maxillary cheek teeth and ventral borders of occipital condyles (taken by placing skull on glass microscope slide with upper incisors rested over edge of slide, and then subtracting thickness of slide).

Statistics

General Protocols: We conducted quantitative analyses to characterize external and cranial morphology and examine nongeographic, geographic, and interspecific variation in Venezuelan *Heteromys*. Statistical analyses were performed with Minitab (2003; version 14.1). To test for any departure from normality in our quantitative data, we conducted Ryan-Joiner tests on the relevant residuals (see below). To correct for multiple unplanned comparisons, we determined significance within families of tests (e.g., within a series of *t*-tests, each comparing the mean between two samples for one of several variables) using Holm's (1979) modification of the Bonferroni procedure. In all other cases, we compared probabilities to an $\alpha = 0.05$. Past studies indicated that sexual dimorphism was insubstantial in the few cases where it was

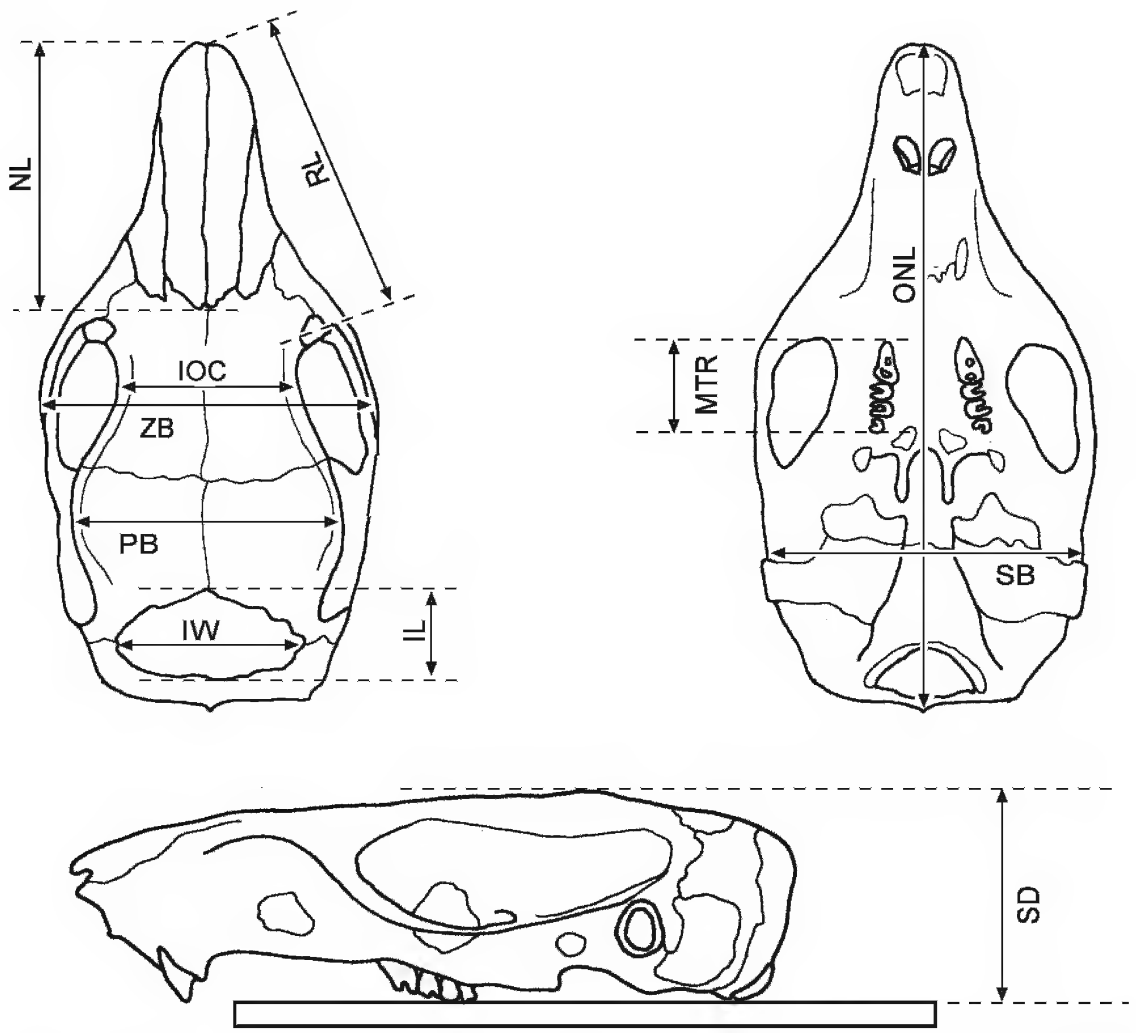

Fig. 2. Dorsal, ventral, and lateral views of a cranium of *Heteromys* showing the methods for taking measurements. Abbreviations and measurements are defined in Materials and Methods.

detected in species of *Heteromys* (Engstrom et al., 1987; Best, 1993). Nevertheless, we test for sexual dimorphism (see Nongeographic and Interspecific Variation); based on the results (see below), males and females were pooled in all other analyses. Species assignments for quantitative analyses were based on our qualitative morphological examinations.

In addition to univariate descriptive and inferential statistics (see below), we conducted principal components analysis (PCA) to examine geographic and interspecific variation from a multivariate perspective. Each PCA was performed on the covariance matrix of log-transformed cranial measurements following Jolicoeur (1963); natural logarithms ($\log_e$ or ln) were used here. PCA is a multivariate-ordination technique that extracts axes of maximum dispersion among observations (here, specimens) without regard to the group (e.g., geographic sample) to which they belong. Each resultant axis (principal component) is characterized by an eigenvector with coefficients that indicate the relationship of each variable (here, cranial measurements) to that multivariate axis. We interpreted the principal components by examination of both coefficients

(elements) of the unit eigenvector and of loadings, which are Pearson product–moment correlation coefficients between specimen scores on each axis and the log-transformed variables. We only interpreted principal components with clearly distinct eigenvalues (by inspection).

GEOGRAPHIC AND INTERSPECIFIC VARIATION (PRIMARY GEOGRAPHIC SAMPLES): We conducted a series of quantitative analyses using eight primary geographic samples of adult *Heteromys* in age class 4 (the most abundant adult age class) from selected sites across northern Venezuela (fig. 1; appendices 1 and 2). The six samples of *H. anomalus* spanned northern Venezuela (*Tukuko*, Estado Zulia, locality 97 of Anderson, 2003b; *Yacambú*, Estado Lara, locality 58 of Anderson, 2003b; *Naiguatá*, Estado Vargas, locality 120; *Neverí*, Estado Sucre, locality 111; *Latal*, Estado Sucre, locality 113; and *Manacal*, Estado Sucre, locality 100). We also included two highland samples from the Cordillera de la Costa representing the putative new highland species (*Rancho Grande*, Estado Aragua, locality 137; and *Humboldt*, Estado Miranda/Estado Vargas, locality 156). These geographic samples were chosen for their relatively large sample sizes and geographic dispersion. Each contains specimens from a single latitude–longitude combination (i.e., specimens with different textual locality descriptions were pooled if they held the same geographic coordinates; appendices 1 and 2; see also Anderson, 2003b). Although specimens of both *H. anomalus* and the new species are known from Naiguatá (localities 120 and 160), only individuals matching the morphological diagnosis of *H. anomalus* are included here in this primary geographic sample (locality 120).

Using specimens from these primary geographic samples, we conducted both univariate and multivariate analyses. First, we calculated descriptive statistics for specimens in age class 4 from each of the eight primary geographic samples, as well as for the two putative species (based on the same individuals but grouped by species rather than by geographic sample). We calculated these statistics for external measurements, mass, cranial measurements, and one derived variable (head-and-body length; table 1, appendix 3). Using these same individuals, we then conducted a series of two-tailed *t*-tests comparing means of the two species for the same measurements and derived variable (these constituted a family for correction for multiple unplanned comparisons). For each variable, we used residuals from these two samples (i.e., after taking species into account) for tests of normality, again correcting for multiple unplanned comparisons. In addition, to test for proportional differences between the species, we examined three ratios of external and cranial variables (tail length/head-and-body length; IOC/ONL; and IW/ONL). Because ratios seldom are distributed normally (Sokal and Rohlf, 1995), we conducted nonparametric tests here (two-tailed Mann-Whitney *U*-test). Finally, to examine the multivariate structure of the data and determine how much of the variation among specimens of the same age class (age class 4) corresponds to geographic and interspecific variation, the 11 cranial measurements for specimens from these samples were submitted to PCA.

NONGEOGRAPHIC AND INTERSPECIFIC VARIATION (SITE OF SYMPATRY): To assess nongeographic variation (including tests for sexual dimorphism) and examine interspecific differences between the species further, we took advantage of one site of sympatry where large samples of both species are available. For Los Canales de Naiguatá (localities 120 and 160), many specimens of each species exist in museum collections; these specimens correspond to all age classes, but age classes 1–4 are especially well represented. Hence, this site provides an opportunity to test for sexual dimorphism (and age-related variation) and examine interspecific variation (across age classes) without the complication of geographic variation in either species. To assess and characterize any differences between the sexes in each species, we performed a two-way General Linear Model (GLM; unbalanced ANOVA) for each cranial measurement, with age class and sex as the two fixed factors (and testing for an interaction term of age class by sex). Here, we used only age classes 1–4, because very few specimens were available in age classes 5 and 6. These GLMs for each species test for differences among the age classes (controlling for sex),

differences between the sexes (controlling for age class), and any possible interactions between age class and sex. This series of GLMs for age class and sex made up a family for correction for multiple unplanned comparisons. Similar to the analyses for the principal geographic samples, we used residuals from these samples (after taking into account both age class and sex) for each variable to test for departures from normality (again correcting for multiple unplanned comparisons).

We assessed interspecific differences at Los Canales de Naiguatá in several ways. First, we calculated descriptive statistics of each species for specimens from this site in each of the age classes 1–4, respectively. We calculated these statistics for all 11 cranial measurements (appendix 4). Second, we performed a second series of two-way GLMs for each cranial measurement, with age class and species as fixed factors, and testing for an interaction term of age class by species. As in the earlier GLMs, we used only age classes 1–4. These analyses test for differences among the age classes (controlling for species), differences between the species (controlling for age class), and any possible interactions between age class and species. This series of GLMs for age class and species formed a family for correction for multiple unplanned comparisons. As above, residuals from these samples (here, after taking into account both age class and species) for each variable were used to test for departures from normality (once again correcting for multiple unplanned comparisons). Third, we performed a PCA using cranial measurements for all available specimens from Los Canales de Naiguatá with intact skulls (age classes 1–6). Because of high levels of variation in interparietal width and interparietal length, those measurements were excluded from this analysis, which was conducted with the remaining nine cranial measurements.

Geographic Variation in the Highland Species: We also performed analyses aimed at assessing geographic variation within the highland species. First, we conducted a PCA on cranial measurements of all specimens of the putative new species in age class 4 with intact skulls (i.e., from all known localities of the species; appendix 1). As above, interparietal width and interparietal length were excluded from this analysis, which was conducted with the remaining nine cranial measurements. We also conducted two-tailed *t*-tests between the primary geographic samples of *Rancho Grande* and *Humboldt* (see above) to detect any difference in mean for each external and cranial measurement (and the derived variable head-and-body length) for specimens in age class 4 (these composed a family for correction for multiple unplanned comparisons). As before, we conducted a Mann-Whitney *U*-test to assess differences between the populations for the tail length/head-and-body length ratio.

SYSTEMATICS

A New Species of *Heteromys* from the Cordillera de la Costa in Venezuela

Our analyses indicate that two species of *Heteromys* exist in central and eastern Venezuela. In this region, *Heteromys anomalus* is widely distributed in fairly mesic lowland areas up to intermediate elevations in the Cordillera de la Costa. The other species is restricted to intermediate and high elevations of the Cordillera de la Costa. It differs externally and cranially from *H. anomalus* and shows differences from all other recognized species of the genus. As no available name exists for this species, we describe it as:

Heteromys catopterius, new species
Overlook Spiny Pocket Mouse
Figures 3, 6, 7, 8, and 9

Holotype: USNM 517536, adult male; skin and skull in excellent condition (fig. 3). Collected on 20 March 1960 from Venezuela: Aragua: Rancho Grande, near Biological Station, 13 km NW Maracay [10°21′N, 67°40′W] at 3576 ft [1090 m] elevation by Charles O. Handley, Jr., and Daniel I. Rhymer; original number COH, Jr. 7778.

Paratypes: We designate as paratypes the following 31 specimens (adults in age class 4; skins and skulls in good condition) from the type locality, and housed in eight museum collections (appendix 1): EBRG 190, 4317; KU 120294, 120295; MCNUSB I-423, 424,

TABLE 1

Descriptive Statistics and Results of Comparisons of Adults in Age Class 4 of *Heteromys anomalus* and *H. catopterius* in Venezuela for External Variables, Mass, and Cranial Measurements

Mean ± standard error, sample size, and observed range (minimum–maximum) are given for each species. Probabilities associated with differences in mean between the two species in two-tailed *t*-tests (or in median for the Mann-Whitney *U*-test, for the tail length/head-and-body length ratio) are indicated as follows: * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$; n.s. = $P > 0.05$. To correct for multiple unplanned comparisons, we determined significance within this family of tests using Holm's (1979) modification of the Bonferroni procedure; here, this altered the statistical conclusion only for hind foot length, which was no longer significant after correction for multiple comparisons. Note that for all significant comparisons, *H. catopterius* averages larger than *H. anomalus*. Linear measurements are in millimeters, mass is in grams, and the ratio is multiplied by 100 to yield a percent.

	H. anomalus	*H. catopterius*
Total length**	289 ± 2, 64 (257–327)	298 ± 2, 37 (270–324)
Head-and-body length (n.s.)	129 ± 1, 65 (115–151)	132 ± 2, 38 (113–149)
Tail length**	160 ± 1, 64 (134–180)	166 ± 2, 35 (147–192)
Tail length/head-and-body length ratio, × 100 (%; n.s.)	124 ± 1, 64 (108–146)	127 ± 2, 35 (100–152)
Hind foot length* (but see table header)	35 ± 0, 65 (31–38)	36 ± 0, 37 (32–39)
Ear length (n.s.)	18 ± 0, 41 (15–22)	19 ± 0, 37 (14–22)
Mass (grams)***	61 ± 2, 40 (42–100)	82 ± 4, 19 (59–119)
Occipitonasal length***	35.37 ± 0.17, 83 (31.06–39.02)	36.64 ± 0.14, 46 (34.74–38.66)
Zygomatic breadth***	16.21 ± 0.07, 83 (14.42–17.90)	16.76 ± 0.10, 46 (15.52–18.17)
Rostral length***	15.66 ± 0.09, 83 (13.60–17.60)	16.29 ± 0.08, 46 (14.98–17.57)
Nasal length***	14.24 ± 0.08, 83 (11.93–16.10)	14.69 ± 0.09, 46 (13.45–15.93)
Least interorbital constriction***	8.38 ± 0.04, 83 (7.66–9.78)	9.13 ± 0.06, 46 (8.13–10.13)
Squamosal breadth***	15.01 ± 0.05, 83 (14.09–16.00)	15.48 ± 0.07, 46 (14.67–16.56)
Maxillary toothrow length***	5.38 ± 0.03, 83 (4.67–6.05)	5.56 ± 0.03, 46 (5.14–5.94)
Interparietal width***	8.74 ± 0.07, 83 (7.06–10.30)	9.42 ± 0.12, 46 (7.72–11.01)
Interparietal length (n.s.)	5.04 ± 0.05, 83 (4.03–5.83)	4.93 ± 0.07, 46 (3.95–6.07)
Parietal breadth***	12.54 ± 0.04, 83 (11.67–13.94)	13.10 ± 0.07, 46 (11.91–14.00)
Skull depth***	11.01 ± 0.03, 83 (10.35–11.65)	11.42 ± 0.05, 46 (10.70–12.07)

581, 1357; MIZA 20-024, 20-028, 20-049, 20-130; UF 13709; UMMZ 110768, 110771; USNM 517533, 517534, 517538–517541, 517543, 517545, 517546, 517558, 517563, 517564, 517566, 517567, 517569; UWZM S.31418.

ETYMOLOGY: The adjective *catopterius* derives from the Greek *katoptêrios* (from *kata*, "down" and *opter*, "eyewitness, scout"; Brown, 1956: 279, 693). *Katoptêrios* was applied to a "height that commands a view" (Liddell and Scott, 1961) in classical texts

Fig. 3. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of the holotype of *Heteromys catopterius* (USNM 517536), an adult male in age class 4. See text and appendix 1 for full provenience.

(e.g., by the geographer Strabo) and is used here as an adjective to mean "commanding a view" or "having a spectacular or wide/panoramic view" (M. Knight, in litt.). We apply this name to the new species in reference to its presence on the rugged and steep-sided Cordillera de la Costa along the littoral of northern Venezuela, from which magnificent views derive, especially of the Caribbean coast. Suitable common names include Overlook Spiny Pocket Mouse (English); and Ratón de Abazones del Mirador, Ratón Bolsero del Mirador, and Ratón Mochilero del Mirador (Spanish).

DISTRIBUTION: Known only from the Cordillera de la Costa of north-central and northeastern Venezuela (figs. 1, 4, 5). The species has been documented from all four major subranges of the Cordillera de la Costa: the main Aragua-Carabobo chain and the El Ávila massif (which together form the Serranía del Litoral), the Serranía del Interior, and the Macizo Oriental. The known elevational range of the species is 350–2425 m, but the vast majority of known records of the species correspond to highland sites above ca. 700 m. See also Sympatry and Zones of Contact with *Heteromys anomalus*, below.

DIAGNOSIS: A species of spiny pocket mouse with adults showing the following combination of characters (figs. 3, 6, 7, 8, 9): p4 (lower permanent premolar) with three lophids; P4 (permanent upper premolar) with straight, moderately long fold in anterior margin of posterior loph; tubercle or swelling at posteroventral border of infraorbital foramen absent; mesopterygoid fossa formed by long, thin hamular processes of pterygoids; optic foramen especially small, with posterior margin formed by strong bar of bone; parietomastoid suture parallel to parietal crest throughout its length; rostrum long and wide (only slightly to moderately tapered anteriorly), without anterodorsal flare; anterior portion of premaxillary convex (inflated), forming a smooth (not stepped) lateral border of rostrum; interorbital constriction wide; braincase wide and moderately inflated; interparietal wide; skull average for genus (ONL 34.74–38.66 mm in adult specimens of age class 4; table 1, appendix 3); dorsal coloration dark slate gray or black and only moderately grizzled with thin ochraceous hairs intermixed among spines; distinctive patch of dark coloration present on dorsal and external surfaces of forearms, continuous with dark coloration of flanks; ears dark gray to black and medium in size; orange band on flanks absent; plantar surface of hind feet naked.

DESCRIPTION: Dorsal pelage (fig. 6) dark slate gray or black (sharply contrasting with soft, white pelage of venter) and moderately grizzled with thin ochraceous hairs intermixed among spines, typically moderately spiny, but soft in some populations; distinctive patch of dark coloration present on dorsal and external surfaces of forearms, continuous with dark coloration of flanks; ventral and internal surfaces of forearms white; orange band on flanks absent; ears dark gray to blackish and medium in size; tail strongly bicolored, and slightly to moderately longer than head-and-body length (table 1, appendix 3); hind feet average for genus (table 1, appendix 3), with plantar surface naked; skull (figs. 3, 7, 8, 9) average for genus (ONL 34.74–38.66 mm in adult specimens of age class 4; table 1, appendix 3); rostrum long and wide (only slightly to moderately tapered anteriorly), without anterodorsal flare; anterior portion of premaxillary convex (inflated), forming a smooth (not stepped) lateral border of rostrum; interorbital region moderately inflated; interorbital constriction wide; braincase wide and moderately inflated; parietal and temporal crests weakly to moderately developed; interparietal variable (moderately wide to very wide), sometimes with distinctive lateral and anterior points; incisive foramina usually short, wide, and anteriorly tapering; tubercle or swelling at posteroventral border of infraorbital foramen absent; mesopterygoid fossa formed by long, thin hamular processes of pterygoids; parapterygoid fossa deep; postalar fissure large and distinctly rounded anteriorly; optic foramen especially small, with posterior margin formed by strong bar of bone; parietomastoid suture parallel to parietal crest throughout its length; anterodorsal lobe of periotic capsule variable in size, sometimes causing notable undulation in posterior margin of squamosal (see Geographic Variation; see schematic drawing in Anderson,

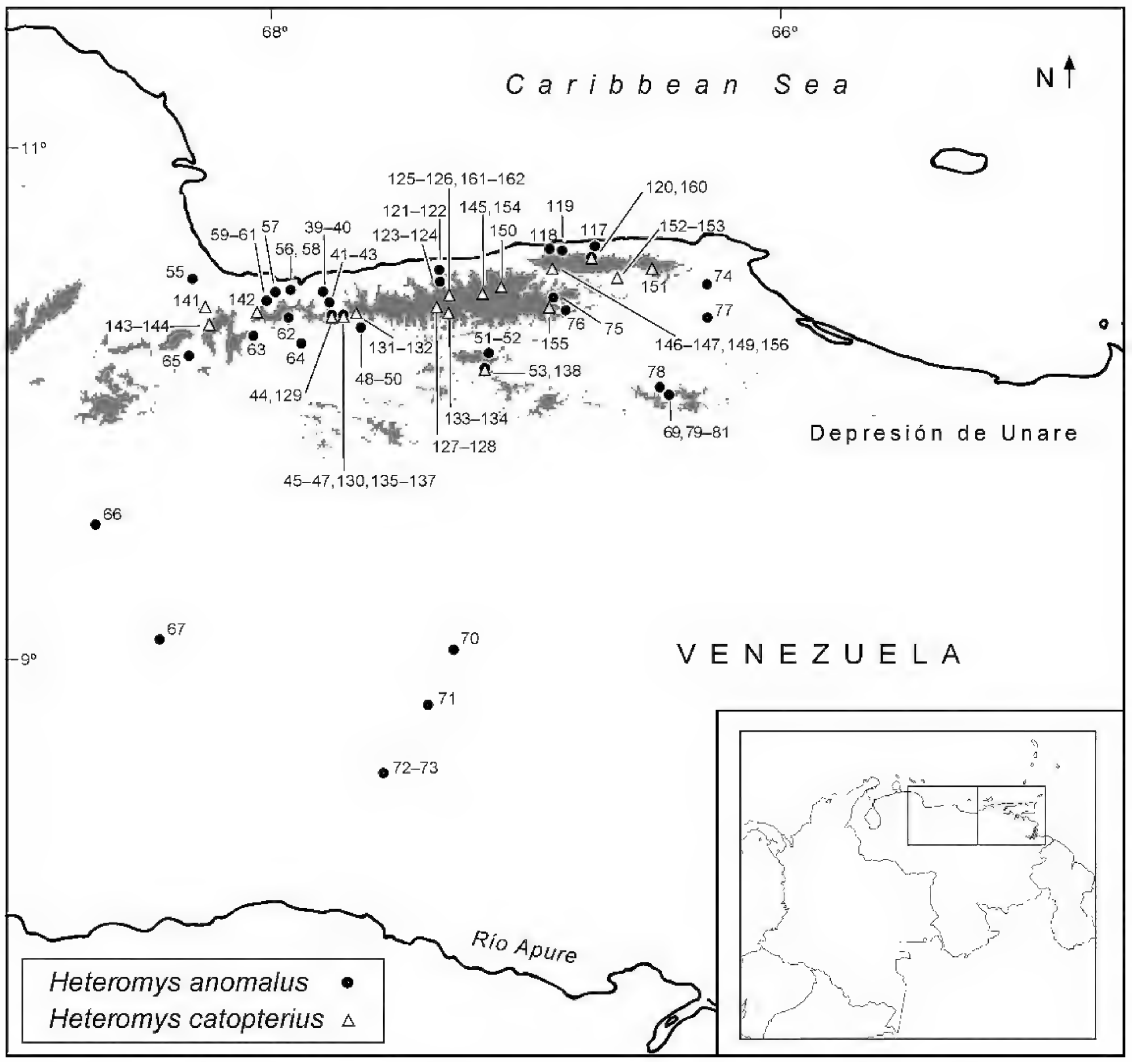

Fig. 4. Maps showing collection localities for *Heteromys* in central and eastern Venezuela and in Trinidad and Tobago. Locality numbers correspond to data given in the Gazetteer (appendix 1). *Heteromys anomalus* continues its distribution to the west (not shown) in northwestern Venezuela, northern Colombia, and the Río Magdalena Valley in central Colombia (see Anderson, 2003b). Only georeferenced localities are plotted here with symbols. Gray shading denotes regions higher than 1000 m in elevation.

1999: 619); jugular foramen (anterolateral to occipital condyle) medium in size; dental formula: (incisors 1/1, canines 0/0, premolars 1/1; molars 3/3) × 2 = total 20; molars variable in size (notably large and robust in some populations but typical for genus in others); lateral borders of lophs of molars smooth, not pointed; lophs of M2 subequal in width; P4 (permanent upper premolar) with straight, moderately long fold in anterior margin of posterior loph, and with smoothly curved posterior border; p4 (lower permanent premolar) with 3 lophids; m3 not reduced, approximately same width as p4.

MEASUREMENTS OF THE HOLOTYPE (mm): total length 321, tail length 186, hind foot length 37, ear length 21, ONL 36.98, ZB 17.52, RL 16.40, NL 15.18, IOC 9.27, SB 16.14, MTR 5.88, IW 10.47, IL 5.08, PB 13.48, SD 11.78. Mass not available.

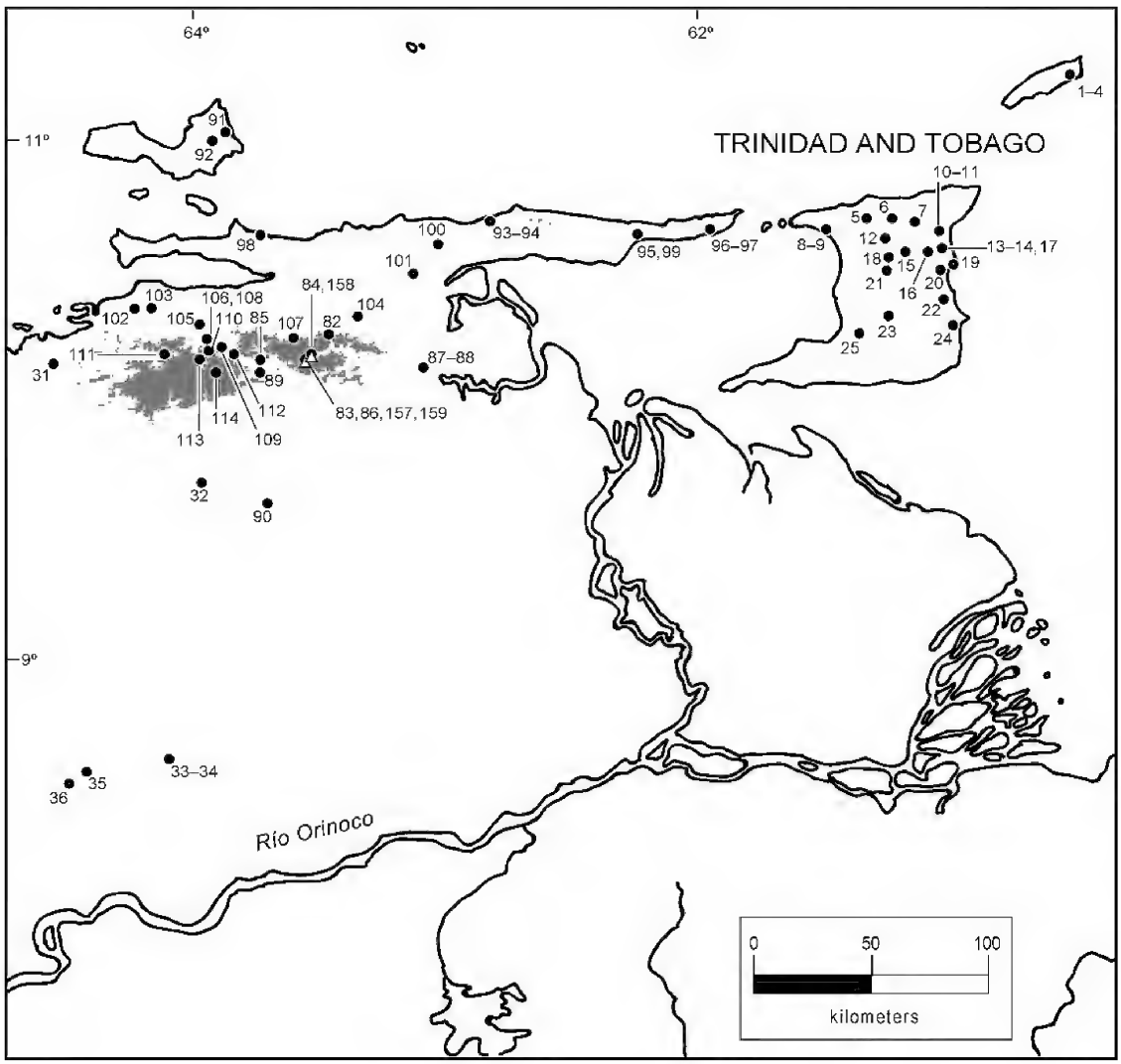

Fig. 4. *(Continued)*

KARYOLOGY: Schmid et al. (1992) reported karyotypic information for three individuals of the species now known as *Heteromys catopterius* from the northern slope of the Cordillera de la Costa along the Maracay–Ocumare de la Costa highway at 940 m in Estado Aragua (locality 130), very near the type locality of Rancho Grande (MIZA 20-391, 20-392, and 20-394; appendix 1). These individuals possessed a standard karyotype with a diploid number of 2n = 60 and a fundamental number of FN = 72. Note, however, that those authors included the four arms of the sex chromosomes in the count for the fundamental number; under standard counting protocols, this karyotype would have a FN = 68 (M. Aguilera, in litt.). Various banding and staining techniques were conducted as well; the Y chromosome shows exceptional quinacrine-positive heterochromatin, indicative of a preponderance of AT-rich sequences (Schmid et al., 1992). Although the standard karyotype of *H. catopterius* is the same as that of *H. anomalus* (see account of that species below), some species of the genus with identical standard karyotypes have been shown to be very distinct based on DNA sequences and morphology (i.e., *H. nubicolens* and nearby populations of *H. desmarestianus*; Anderson

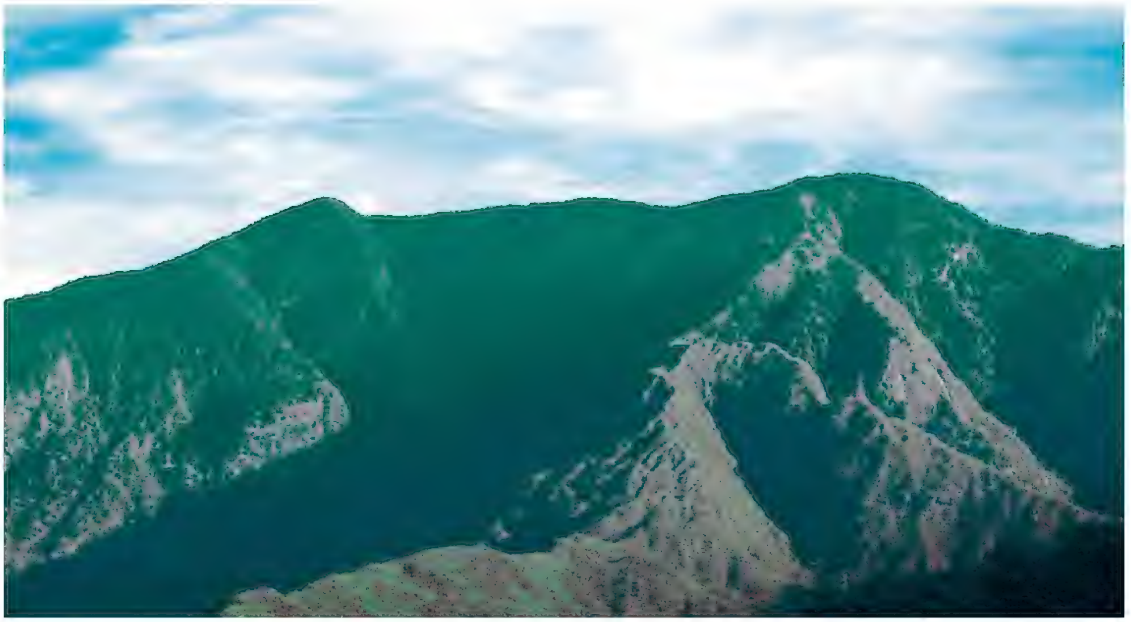

Fig. 5. Landscape on the southern slopes of the Serranía del Litoral of the Cordillera de la Costa in Estado Carabobo and Estado Aragua. Here, *Heteromys catopterius* inhabits areas above ca. 1000 m (principally cloud forests), and *H. anomalus* occurs in other forested areas at lower elevations. Rancho Grande (locality 137), the type locality of *H. catopterius*, lies near the western peak. Photographed by Eliécer E. Gutiérrez in January 2008, from the northern outskirts of the city of Maracay.

Fig. 6. Dorsal external morphology of adult male specimens in age class 4 of two species of *Heteromys* from the Rancho Grande/El Limón region in Estado Aragua, Venezuela, illustrating interspecific variation based on samples in close geographic proximity: *Heteromys catopterius* (top), Rancho Grande, near Biological Station, 13 km NW Maracay, 3576 ft [1090 m] (USNM 517536; holotype of *Heteromys catopterius*; locality 137) and *H. anomalus* (bottom), Rancho Grande [region], El Limón, 4 km NW Maracay, 524 m (USNM 517544; locality 50).

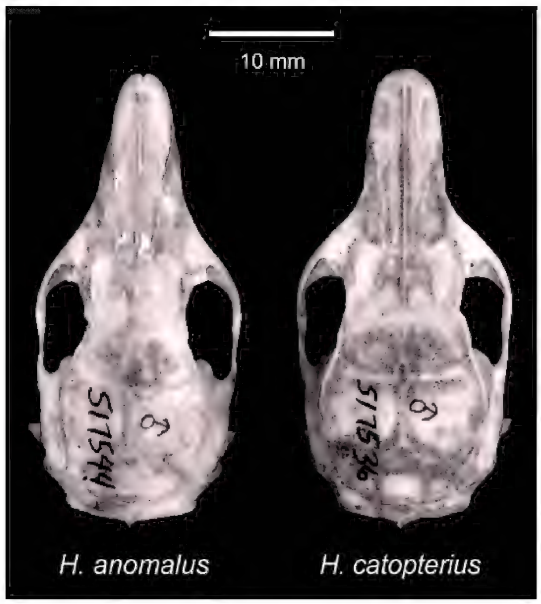

Fig. 7. Dorsal views of the crania of adult male specimens in age class 4 of two species of *Heteromys* from the Rancho Grande/El Limón region in Estado Aragua, Venezuela, illustrating interspecific variation based on samples in close geographic proximity: *Heteromys anomalus*, Rancho Grande [region], El Limón, 4 km NW Maracay, 524 m (left, USNM 517544; locality 50) and *H. catopterius*, Rancho Grande, near Biological Station, 13 km NW Maracay, 3576 ft [1090 m] (right, USNM 517536; holotype of *Heteromys catopterius*; locality 137).

et al., 2006; Anderson and Timm, 2006; Anderson and Jansa, 2007); future banding studies are necessary to compare the cytogenetics of *H. catopterius* and *H. anomalus* in more detail.

Comparisons: Externally, the dark slate-gray dorsal pelage (only moderately grizzled with ochraceous hairs; fig. 6) of *Heteromys catopterius* differentiates it from most currently recognized species of the genus. Three types of dorsal pelage are present in the genus (pale brown, strongly grizzled; dark brown, moderately grizzled; and dark slate gray, nearly uniform to moderately grizzled). In contrast to the new species, *Heteromys gaumeri*, *H. oasicus*, and most populations of *H. anomalus* have pale brown dorsal pelage that is strongly grizzled with thin ochraceous hairs intermixed among the spines (Anderson, 2003b). In addition, specimens of *H. gaumeri* possess an orange band on the flanks that is absent in *H. catopterius*. The dwarf species *H. oasicus* is much smaller than *H. catopterius* (total length 227–250 mm for adults in age class 4; Anderson 2003b). *Heteromys gaumeri* is restricted geographically to Belize, Guatemala, and the Península de Yucatán in Mexico (Williams et al., 1993). *Heteromys oasicus* inhabits only the Península de Paraguaná in northwestern Venezuela, to the northwest of known records of *H. catopterius* (Anderson, 2003b). *Heteromys anomalus* inhabits much of northern South America and comes into geographic contact with *H. catopterius* in several areas; because the pelage of *H. anomalus* is atypically dark in a few portions of its range (i.e., similar to that of *H. catopterius*), detailed comparisons are necessary to ensure proper identification (see below). The pelage of *H. catopterius* also differs from the dark-brown pelage of *H. nubicolens* and members of the *H. desmarestianus* species complex, which occur in Mexico and Central America far from the known distribution of *H. catopterius* (Anderson and Timm, 2006; *H. d. crassirostris* also has a marginal distribution in South America in extreme northwestern Colombia; Anderson, 1999).

Heteromys catopterius shares dark slate-gray pelage with several other species of the genus (*H. australis*, *H. nelsoni*, *H. oresterus*, and *H. teleus*). Both *H. nelsoni* and *H. oresterus* display extremely soft dorsal pelage, in contrast to the pelage of *H. catopterius*, which is spiny in most populations (all known populations except those from the Macizo Oriental). They are distributed in restricted highland regions of extreme southeastern Mexico and southwestern Guatemala (*H. nelsoni*) and the Cordillera de Talamanca in Costa Rica (*H. oresterus*; Rogers and Rogers, 1992; Williams et al., 1993; Reid, 1997), respectively. *Heteromys teleus* and *H. australis* are extremely similar to *H. catopterius* externally, although their pelage tends to be even darker than that of *H. catopterius*. Like the new species, they also inhabit South America but are not known to come into geographic contact with it. *Heteromys teleus* is endemic to western Ecuador, and the distribution of *H. australis* extends from

Fig. 8. Dorsal views of the crania of specimens of *Heteromys catopterius* from the Rancho Grande region (Estado Aragua) in several age classes, showing growth-related differences in size and shape. All specimens derive from localities 131 and 137, only ca. 2 km distant from each other at elevations of 3576–4900 ft [1090–1494 m] (USNM 517550, age class 1; USNM 517549, age class 2; USNM 517536, age class 4; USNM 562956, age class 5). Such marked differences among age classes are typical of species of the genus (see Anderson and Timm, 2006: 14) and complicate identification and characterization of nongeographic, geographic, and interspecific variation. See appendix 1 for full provenience.

northwestern Ecuador and extreme eastern Panama through much of Colombia to western Venezuela; Anderson, 1999, 2003b; Anderson and Jarrín-V., 2002). Cranial characters are necessary to distinguish them from *H. catopterius*.

Cranial characters serve to separate *Heteromys catopterius* from all other species of the genus (figs. 3, 7, 8, 9). *Heteromys catopterius* differs from *H. gaumeri* by the narrow postalar fissure and deeply concave (collapsed) anterior termination of the premaxillary of *H. gaumeri*. Additionally, the form of the premaxillary in *H. gaumeri* creates a distinct step in the lateral border of the rostrum in dorsal view, a character lacking in the new species (Anderson et al., 2006). *Heteromys catopterius* contrasts with the Central American and Mexican species *H. desmarestianus*, *H. nelsoni*, *H. nubicolens*, and *H. oresterus* by its especially small optic foramen and straight, only moderately long fold in the anterior margin of the posterior loph of P4. Consistent, but more subtle, differences exist in comparison with other South American species. *Heteromys oasicus* is much smaller than the new species and has a much less-developed rostrum (Anderson, 2003b). In comparison with *H. catopterius*, the braincase of *H. australis* is even more inflated and the rostrum less developed. *Heteromys teleus* is very similar to the new species cranially but has wider (bowed) zygomatic arches and an uninflated braincase. These three species inhabit areas of South America to the west of the known distribution of *H. catopterius*. Cranial differences also separate *H. catopterius* from *H. anomalus* (see detailed comparisons below).

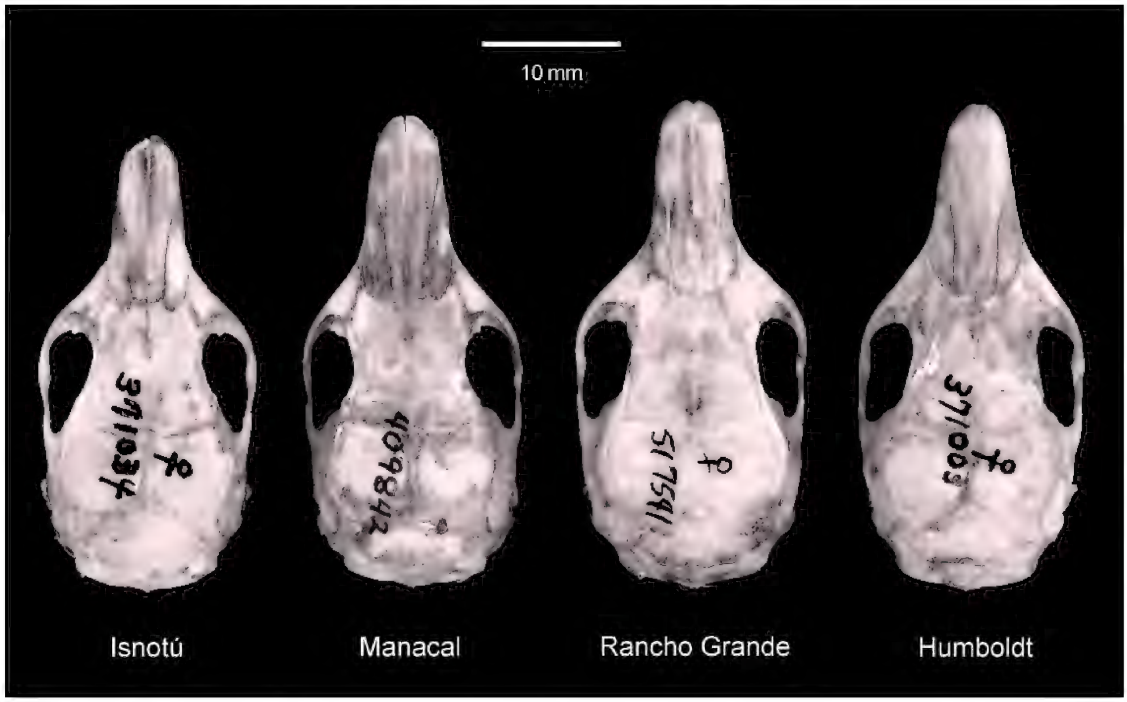

Fig. 9. Dorsal views of the crania of adult female specimens in age class 4 of *Heteromys anomalus* (two crania on left) and *H. catopterius* (two crania on right) from Venezuela, showing interspecific and geographic variation: *H. anomalus* from 10 km WNW Valera, Isnotú, 930 m (Estado Trujillo; locality 82 in Anderson, 2003b) and 5 km S and 25 km E Carúpano, Manacal, 185 m (Estado Sucre; locality 100) and *H. catopterius* from Rancho Grande, near Biological Station, 13 km NW Maracay, 3576 ft [1090 m] (Estado Aragua; locality 137) and Hotel Humboldt, 9.4 km N Caracas, 2181 m (Estado Miranda/Estado Vargas; locality 156). See appendices 1 and 2 for full provenience.

External differences exist between *Heteromys catopterius* and *H. anomalus*. Externally, most populations of *H. anomalus* have a pale brown dorsal pelage that is strongly grizzled with thin ochraceous hairs, in stark contrast to the dark slate-gray dorsal pelage (only moderately grizzled with ochraceous hairs) of *H. catopterius*. In addition, *H. catopterius* possesses a distinctive patch of gray or black on the forearm; the homologous patch is present in *H. anomalus* as well, but it is typically paler and brownish. However, some populations of *H. anomalus* from mesic areas (e.g., some regions of Estados Lara, Monagas, Sucre, and Zulia in Venezuela, and the island of Tobago in Trinidad and Tobago) exhibit a much darker dorsal pelage, very similar to that of *H. catopterius* in general aspect and in the coloration of the patch on the forearm. Notably, however, *H. anomalus* has distinctively rounded ears throughout its range, in contrast to *H. catopterius* and all other species of the genus (which have moderately pointed ears). Additionally, *H. catopterius* has much longer, darker mystacial vibrissae than *H. anomalus* (fig. 6).

Cranial differences in size and shape also distinguish *Heteromys catopterius* from *H. anomalus*. Overall, the skull of the new species is larger than that of *H. anomalus* and relatively wider (less elongated). Regarding proportional differences, *H. catopterius* generally shows a more inflated braincase, a relatively wider interorbital constriction, and a relatively wider interparietal. In addition, it tends to possess wider (often short and anteriorly tapering) incisive foramina (the incisive foramina of *H. anomalus* vary geographically but tend to be longer, thinner, and more parallel sided than those of *H. catopterius*).

The analyses of nongeographic variation in cranial measurements at Los Canales de Naiguatá documented strong age-related differences but no sexual dimorphism. The GLMs of individuals of *H. anomalus* in age classes 1–4 showed highly significant age-related differences for all variables but maxillary toothrow length, interparietal width, and interparietal length ($P < 0.002$ for significant comparisions; $P = 0.152$ for IW; $P = 0.312$ for IL; $P = 0.003$ for MTR, not significant after correction for multiple comparisons). Sex was not significant for any variable ($P = 0.023$ for ZB; $P = 0.045$ for IOC, neither significant after correction for multiple comparisons; $P = 0.080$–0.779 for other nonsignificant comparisons). No interaction term was significant ($P = 0.064$–0.451). Furthermore, no variable showed a departure from normaility ($P > 0.058$). Results for *H. catopterius* were similar. For this species, age class was significant for all variables but interparietal width, interparietal length, and parietal breadth ($P < 0.002$ for significant comparisions; $P = 0.107$ for IL; $P = 0.007$ for IW; $P = 0.006$ for PB, neither of the latter two significant after correction for multiple comparisons). Sex was never significant ($P = 0.486$–0.992), nor was any interaction term ($P = 0.042$ for PB, not significant after correction for multiple comparisons; $P = 0.376$–0.996 for other nonsignificant comparisons). As in the tests for *H. anomalus*, no variable showed a departure from normaility ($P = 0.040$ for SB; $P = 0.030$ for MTR, neither significant after correction for multiple comparisons; $P > 0.079$ for other nonsignificant comparisons).

Quantitative comparisons documented differences in size and shape between *Heteromys catopterius* and *H. anomalus*. Even though the two species overlapped for mass and all external and cranial variables (for specimens in age class 4 from the primary geographic samples), means were significantly different for some external variables, mass, and most cranial variables (but no variable showed a departure from normality; $P = 0.040$ for mass; $P = 0.030$ for IOC, neither significant after correction for multiple comparisons; $P > 0.100$ for other nonsignificant comparisons). For external variables and mass, only total length, tail length, and mass were significant ($P < 0.005$ for significant comparisons; $P = 0.147$ for head-and-body length; $P = 0.171$ for ear length; $P = 0.025$ for hind foot length, not significant after correction for multiple comparisons; table 1). The corresponding test for a difference in median for the tail length/head-and-body length ratio was not significant ($P = 0.090$). All cranial measurements except interparietal length showed significant differences in mean between the two species ($P < 0.001$ for significant comparisons; $P = 0.200$ for IL; table 1). For all significant comparisons, *H. catopterius* averaged larger than *H. anomalus* (see also figs. 7, 9). Regarding differences in cranial shape, *H. catopterius* showed a relatively wider interorbital constriction and relatively wider interparietal (IOC/ONL ratio, $P < 0.001$; IW/ONL ratio, $P = 0.007$).

Quantitative analyses document similar differences between *Heteromys catopterius* and *H. anomalus* at a site of sympatry. At Los Canales de Naiguatá, both species and age class were important factors (but no variable showed a departure from normality; $P = 0.041$ for MTR, not significant after correction for multiple comparisons; $P > 0.086$ for other nonsignificant comparisons). These GLMs for age classes 1–4 documented that the species were significantly different for all cranial measurements but interparietal width and interparietal length ($P < 0.001$ for significant comparisions; $P = 0.210$ for IL; $P = 0.035$ for IW, not significant after correction for multiple comparisons). Age class was significant for all measurements but IW ($P < 0.004$ for significant comparisons; $P = 0.005$ for IW, not significant after correction for multiple comparisons), but no interaction term was significant ($P = 0.393$–0.991). *Heteromys catopterius* averaged larger than *H. anomalus* for all measurements that were significantly different.

Multivariate analyses also supported the morphological distinctiveness of *Heteromys catopterius* from *H. anomalus*. In a plot of scores on the first two principal components of the PCA undertaken on specimens in age class 4 from the primary geographic samples, substantial but incomplete overlap occurred between specimens of the two species (fig. 10). The coefficients and loadings of PC1 were all of the same sign, indicating that

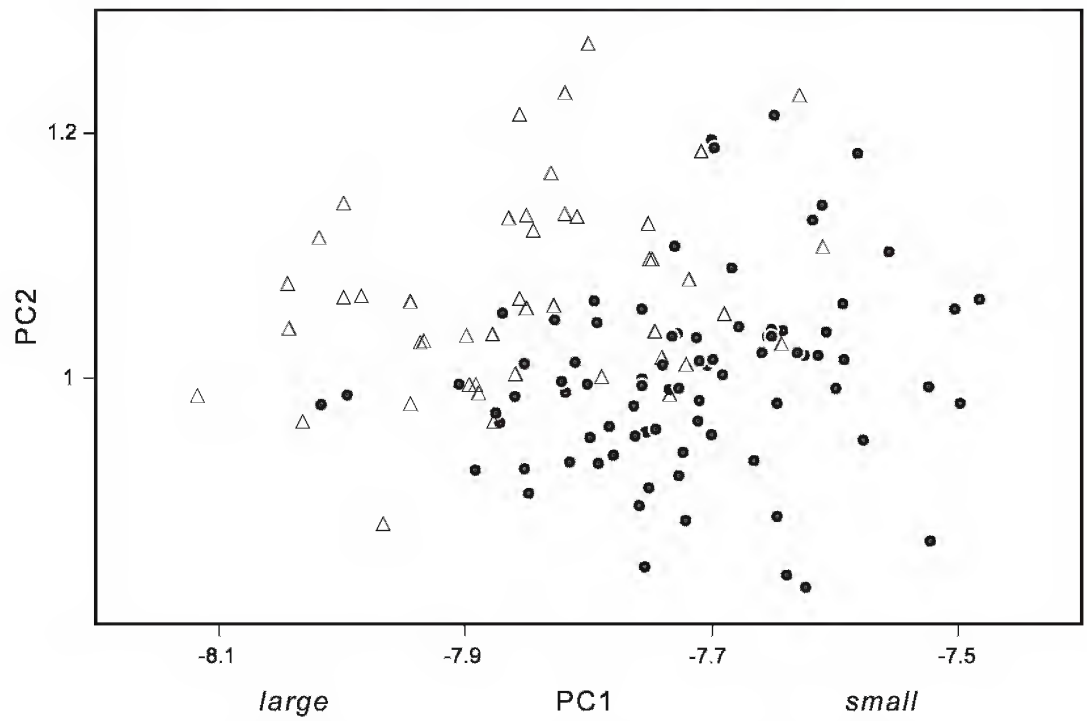

Fig. 10. Plot of specimen scores on the first two axes of the principal components analysis of 11 cranial measurements of adult specimens of *Heteromys* in age class 4 from the eight primary geographic samples across northern Venezuela. Specimens of *H. anomalus* are marked by circles, and individuals of *H. catopterius* are denoted by triangles. PC1 is a size axis (with larger specimens appearing toward the left side of the plot), and PC2 represents a shape difference (see text and table 2).

TABLE 2

Results of Principal Components Analysis of Adult Specimens in Age Class 4 of *Heteromys anomalus* and *H. catopterius* from Primary Geographic Samples across Northern Venezuela (see fig. 10)

Elements of the unit eigenvector and loadings are presented for the first three principal components. Eleven cranial measurements were transformed to their natural logarithms (ln) before computation of the covariance matrix and extraction of components. Eigenvalues (multiplied by 100) and the percentage of variation among specimens explained are given for each axis.

	Unit eigenvector			Loadings		
	PC1	PC2	PC3	PC1	PC2	PC3
ln-Occipitonasal length	−0.263	0.079	−0.263	−0.815	0.161	−0.443
ln-Zygomatic breadth	−0.294	0.070	−0.118	−0.872	0.136	−0.190
ln-Rostral length	−0.274	0.162	−0.351	−0.725	0.283	−0.506
ln-Nasal length	−0.296	0.129	−0.371	−0.733	0.211	−0.500
ln-Least interorbital constriction	−0.384	0.270	−0.020	−0.817	0.378	−0.023
ln-Squamosal breadth	−0.205	0.066	−0.015	−0.820	0.174	−0.033
ln-Maxillary toothrow length	−0.221	0.097	−0.175	−0.585	0.169	−0.252
ln-Interparietal width	−0.491	0.021	0.762	−0.752	0.021	0.636
ln-Interparietal length	−0.322	−0.922	−0.150	−0.465	−0.876	−0.118
ln-Parietal breadth	−0.229	0.022	0.145	−0.763	0.048	0.262
ln-Skull depth	−0.216	0.085	0.002	−0.830	0.215	0.004
Eigenvalue (× 100)	1.645	0.711	0.487			
% variation explained	49.7	21.5	14.7			

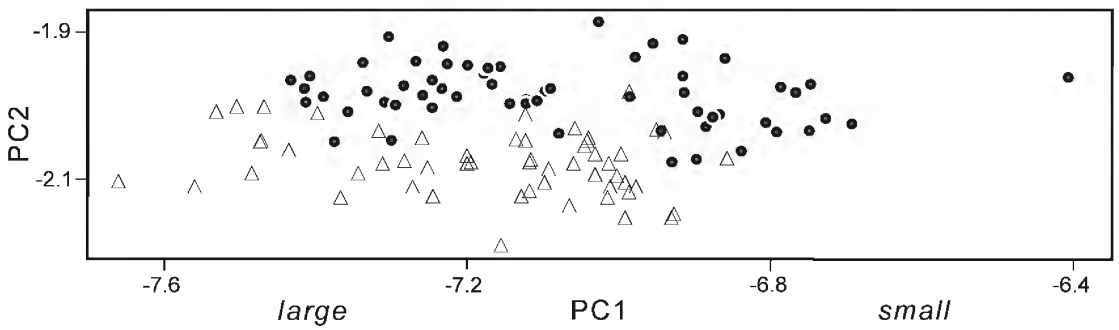

Fig. 11. Plot of specimen scores on the first two axes of a principal components analysis of nine cranial measurements of specimens of *Heteromys anomalus* (circles) and *H. catopterius* (triangles) in all age classes from Los Canales de Naiguatá (localities 120 and 160). PC1 represents a size axis (with larger specimens appearing toward the left side of the plot), and PC2 portrays a difference in shape (see text and table 3).

it represented a size axis (with larger specimens having lower scores, because the signs of the coefficients were all negative; table 2). In contrast, PC2 represented a shape axis (because most coefficients were positive, but that of interparietal length was negative; table 2).

Multivariate differences between the two species were much clearer when considering specimens from only one site. At Los Canales de Naiguatá, only very limited overlap between *Heteromys catopterius* and *H. anomalus* existed in a plot of scores on the first two principal components of the PCA undertaken on specimens in all age classes (using all cranial measurements but interparietal width and interparietal length; fig. 11). As above, the coefficients and loadings of PC1 were all of the same sign, indicating that it represented a size axis (again with larger specimens showing lower scores, since the signs of all the coefficients were negative; table 3). Here, PC2 again constituted a shape axis (because some coefficients were positive and others negative; table 3), but the axis was very different than the one for the PCA for the primary geographic samples. At Los Canales de Naiguatá, PC2 represented a contrast between occipitonasal length, rostral length, and nasal length vs. zygomatic breadth, least interorbital constriction, squamosal breadth, maxillary toothrow length, parietal breadth, and skull depth. Specimens with larger values for the former three measurements relative to their values for the latter ones showed larger (less negative) scores on this axis. This analysis indicated strong shape differences between the two species, with *H. anomalus* more elongated than the relatively wider *H. catopterius*. Accordingly, a bivariate plot of least interorbital constriction vs. nasal length (fig. 12) showed a clear difference in shape between the two species: with very little overlap, specimens of *H. anomalus* exhibited a longer nasal length relative to least interorbital constriction (and individuals of *H. catopterius* showed a wider least interorbital constriction relative to nasal length).

In sum, the quantitative analyses indicate that adult *Heteromys catopterius* were larger in overall body size than those of *H. anomalus* and differed in cranial proportions (figs. 7, 9, 10, 11, 12). Almost all measurements averaged larger for *H. catopterius*, table 1, appendices 3 and 4). Furthermore, *H. catopterius* showed a relatively wider, less-elongated skull (with relatively wider interorbital constriction and interparietal). These differences in shape were also evident in direct visual examination of skulls.

GEOGRAPHIC VARIATION: Quantitative analyses indicated notable geographic variation between samples of *Heteromys catopterius* from western vs. central portions of its range (appendix 3). Means for most variables were significantly different in univariate comparisons of specimens from Rancho Grande (locality 137) with those from Humboldt (locality 156). Externally, all variables but tail length ($P = 0.057$) were significant ($P <$

TABLE 3
Results of Principal Components Analysis of Interspecific Variation Between *Heteromys anomalus* and *H. catopterius* Based on Specimens in All Age Classes from Los Canales de Naiguatá (see fig. 11)

Elements of the unit eigenvector and loadings are presented for the first three principal components. Nine cranial measurements were transformed to their natural logarithms (ln) before computation of the covariance matrix and extraction of components. Eigenvalues (multiplied by 100) and the percentage of variation among specimens explained are given for each axis.

	Unit eigenvector			Loadings		
	PC1	PC2	PC3	PC1	PC2	PC3
ln-Occipitonasal length	−0.401	0.045	−0.043	−0.989	0.032	−0.016
ln-Zygomatic breadth	−0.287	−0.219	0.133	−0.933	−0.205	0.066
ln-Rostral length	−0.501	0.173	−0.081	−0.985	0.098	−0.024
ln-Nasal length	−0.529	0.531	0.000	−0.955	0.275	0.000
ln-Least interorbital constriction	−0.298	−0.496	0.308	−0.870	−0.417	0.138
ln-Squamosal breadth	−0.214	−0.079	0.185	−0.916	−0.097	0.121
ln-Maxillary toothrow length	−0.199	−0.419	−0.860	−0.742	−0.450	−0.491
ln-Parietal breadth	−0.101	−0.433	0.291	−0.546	−0.672	0.240
ln-Skull depth	−0.204	−0.153	0.144	−0.910	−0.197	0.099
Eigenvalue (× 100)	4.704	0.389	0.110			
% variation explained	86.7	7.2	2.0			

0.003 for significant comparisons; test for mass not possible). The populations did not differ in median for the tail length/head-and-body length ratio ($P = 0.414$). Comparisons of cranial measurements indicated that averages were significantly different for all measurements but rostral length and maxillary toothrow length ($P = 0.051$ for MTR; $P = 0.025$ for RL, not significant after correction for multiple comparisons; $P < 0.006$ for

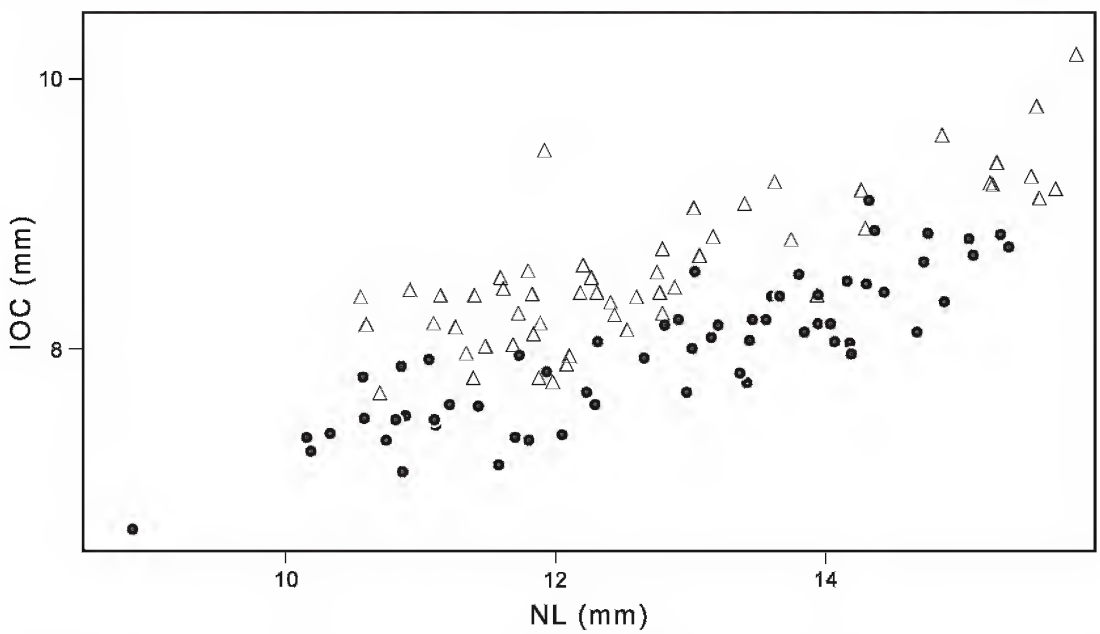

Fig. 12. Plot of least interorbital constriction vs. nasal length for specimens of *Heteromys* in all age classes from Los Canales de Naiguatá (localities 120 and 160). Circles represent individuals of *H. anomalus*, and triangles denote those of *H. catopterius*. Note that specimens of *H. catopterius* have a wider interorbital constriction than those of *H. anomalus*, relative to the length of their nasals.

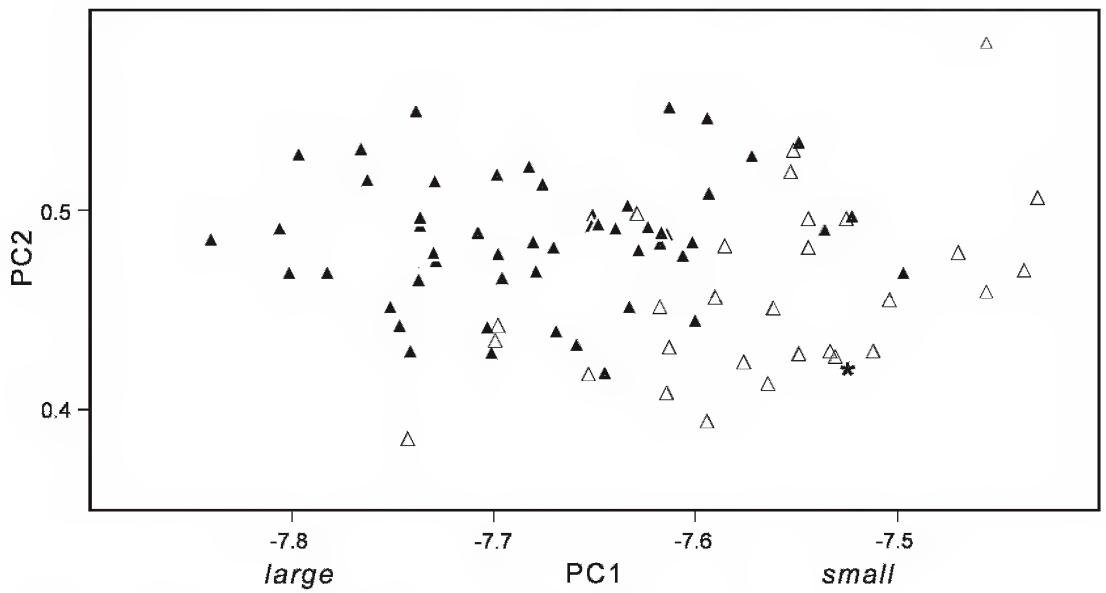

Fig. 13. Plot of specimen scores on the first two axes of a principal components analysis of nine cranial measurements of adult specimens of *H. catopterius* in age class 4 from throughout the range of the species. Solid triangles denote specimens from Estado Carabobo and western Estado Aragua; open triangles indicate specimens from eastern Estado Aragua as well as those from Estado Miranda, Estado Vargas, and Distrito Capital; and the asterisk represents the lone specimen from Estado Monagas. PC1 represents a size axis (with larger specimens appearing toward the left side of the plot), and PC2 constitutes a shape difference (see text and table 4).

significant comparisons). For all variables with a significant difference, the sample from Rancho Grande averaged larger than the one from Humboldt.

Multivariate morphometric analysis also showed substantial differences between westernmost populations vs. central and eastern ones. A plot of scores on the first two principal components of the PCA undertaken on all available specimens of *Heteromys catopterius* in age class 4 (using all cranial measurements but interparietal width and interparietal length) summarized morphometric variation within the new species (fig. 13). Only moderate overlap existed between specimens from westernmost populations (from Estado Carabobo and western portions of Estado Aragua, in the vicinity of Rancho Grande) vs. those from the El Ávila massif (the central portion of the species' distribution; figs. 1, 4). The lone available specimen from Estado Monagas in northeastern Venezuela (from the Macizo Oriental) lay within the cloud of specimens from El Ávila. Specimens from geographically intermediate populations in eastern Estado Aragua, western Estado Miranda, western Estado Vargas, and western Distrito Capital (e.g., Alto Ñeo León, Pico Codazzi, and El Laurel; appendix 1) tended to group with the central populations (from the El Ávila massif). These geographically intermediate populations lie to the west of the depression separating the El Ávila massif from the main Aragua-Carabobo chain of the Serranía del Litoral; this depression is marked by the courses of the Quebrada Tacagua and the Río Guaire. Individuals from the Serranía del Interior also fell with this group (Campamento Rafael Rangel; east-central Estado Aragua). The coefficients and loadings of PC1 all possessed the same sign, signifying that it represented a size axis (with larger specimens showing lower scores, because the signs of all the coefficients were negative; table 4). In contrast, PC2 constituted a shape axis (because some coefficients were positive and others negative; table 4). Here (as in the PCA for Los Canales de Naiguatá), PC2 represented a contrast between occipitonasal

TABLE 4
Results of Principal Components Analysis of Geographic Variation in *Heteromys catopterius* Based on Adult Specimens in Age Class 4 from throughout the Range of the Species (see fig. 13)
Elements of the unit eigenvector and loadings are presented for the first three principal components. Nine cranial measurements were transformed to their natural logarithms (ln) before computation of the covariance matrix and extraction of components. Eigenvalues (multiplied by 100) and the percentage of variation among specimens explained are given for each axis.

	Unit eigenvector			Loadings		
	PC1	PC2	PC3	PC1	PC2	PC3
ln-Occipitonasal length	−0.324	−0.238	−0.086	−0.895	−0.279	−0.080
ln-Zygomatic breadth	−0.375	0.194	0.020	−0.903	0.197	0.016
ln-Rostral length	−0.367	−0.461	−0.093	−0.830	−0.441	−0.071
ln-Nasal length	−0.427	−0.468	0.065	−0.851	−0.394	0.044
ln-Least interorbital constriction	−0.452	0.201	0.210	−0.876	0.165	0.138
ln-Squamosal breadth	−0.230	0.265	0.208	−0.724	0.353	0.222
ln-Maxillary toothrow length	−0.249	0.343	−0.880	−0.598	0.348	−0.715
ln-Parietal breadth	−0.202	0.475	0.310	−0.593	0.590	0.308
ln-Skull depth	−0.277	0.143	0.145	−0.843	0.184	0.149
Eigenvalue (× 100)	0.847	0.152	0.097			
% variation explained	66.0	11.8	7.6			

length, rostral length, and nasal length vs. zygomatic breadth, least interorbital constriction, squamosal breadth, maxillary toothrow length, parietal breadth, and skull depth. Specimens with smaller values for the former three measurements relative to their values for the latter ones showed larger (more positive) scores on this axis.

Visual morphological observations indicate that subtle differences exist between the westernmost populations of *Heteromys catopterius* and the central and eastern populations of the species, but geographically intermediate localities appear to show transitional morphologies. Specimens from localities in Estado Carabobo and from the Rancho Grande region of Estado Aragua are generally larger and relatively wider than those from the El Ávila massif and from the Macizo Oriental, which are more elongated in shape (but not as much as *H. anomalus*). In addition, the rostrum is more developed and parallel sided (not anteriorly tapering) in western populations, in contrast to the somewhat less massive and slightly tapering rostrum typical of central and eastern populations. Two further differences distinguish the Rancho Grande population from that of Humboldt: (1) the molars appear larger and more robust in Rancho Grande than in Humboldt and (2) at Rancho Grande, the anterodorsal lobe of the periotic capsule of the mastoid is large, causing a distinct undulation in the posterior border of the squamosal, whereas this lobe is small at Humboldt, not causing a notable undulation in the posterior border of the squamosal. Despite these noteworthy differences between specimens from the two regions, individuals from sites geographically between Rancho Grande and Humboldt, in eastern Estado Aragua, western Estado Miranda, western Estado Vargas, and western Distrito Capital (e.g., Pico Codazzi, Alto Ñeo León; appendix 1), exhibit intermediate morphologies but generally match the central and eastern populations more closely than they do the more-western populations. Finally, one character distinguishes the populations in the Macizo Oriental from all others: individuals there possess very soft dorsal pelage, in contrast to the spiny pelage of western and central populations.

NATURAL HISTORY: Published studies and field notes provide rich and varied ecological information on *Heteromys catopterius*. Most of the available information corresponds to two sites where it has been collected in large numbers in the Serranía del Litoral (fig. 1): the vicinity of Rancho Grande in Estado

Fig. 14. Habitat of *Heteromys catopterius* at Rancho Grande (locality 137), Estado Aragua, Venezuela, taken just above the Estación Biológica. Photographed by Eliécer E. Gutiérrez in January 2008.

Aragua and the area surrounding Hotel Humboldt on the El Ávila massif along the border between Estado Miranda and Estado Vargas. Further information derives from sites in the Río Morón drainage on the northern slopes of the Cordillera de la Costa in Estado Carabobo (Bisbal-E., 1993). Unfortunately, the extensive morphological, reproductive, developmental, and behavioral information for *Heteromys* at Los Canales de Naiguatá in Estado Vargas in the Serranía del Litoral presented by Valdez et al. (1985) derives from a pooling of approximately equal numbers of *H. catopterius* and *H. anomalus* (appendix 1); future reanalysis of those data could provide fascinating insights into the ecology of the two species at this site of sympatry, but natural history information from that site is not included here.

At Rancho Grande near the crest of the main range of the Serranía del Litoral in Estado Aragua (fig. 14), field notes and specimen tags indicate that the species was captured commonly in various forested habitats but not in grassy and brushy areas. In the region surrounding the Estación Biológica de Rancho Grande (localities 131, 132, 136, and 137, Estado Aragua), Charles O. Handley, Jr. and Daniel I. Rhymer (assisted occasionally by John P. Rood) caught *H. catopterius* frequently in several habitats in March and April of 1960 (C.O. Handley, Jr. field notes, 1960; specimen tags). These habitats include: (1) an area of secondary vegetation below the Estación Biológica in an abandoned coffee and banana farm (although traps were placed there in areas grown up with weeds, grass, and brush, as well as in "dry" forest, evidently *Heteromys* were captured only in the forested areas, termed "deciduous forest" on specimen tags); (2) a forested (presumably evergreen) area on the slope behind the Estación Biológica along the "water trail" (see map in Beebe and Crane, 1947: 48; (3) forested areas (including cloud forest) at El Portachuelo, slightly below and west of the Estación Biológica; and (4) cloud forest on Pico Limón. Although traps were placed in grassy areas near the Estación Biológica, *Heteromys* was not captured there.

The month following completion of work at Rancho Grande by Handley and Rhymer, John P. Rood conducted capture-recapture sampling and laboratory experiments at Rancho Grande that provide extensive information regarding the ecology, behavior, and development of *Heteromys catopterius* (Rood, 1963; Rood and Test, 1968). Rood collected a few voucher specimens from these trapping grids and adjacent areas (see Rood and Test, 1968); all that we have examined represent *H. catopterius* (appendix 1). Approximately half derive from cloud forest, but others were captured in a forest near a small stream, a second-growth forest, second growth at the edge of tall grass, and a clump of tall grass near second-growth forest (J.P. Rood field notes, 1960). Although some of the individuals in Rood's studies may have been *H. anomalus* (which has been captured occasionally at Rancho Grande; see Sympatry and Zones of Contact with *Heteromys anomalus*), at least the vast majority probably were the species now known as *H. catopterius*.

Rood sampled two areas using traps arranged in grids (Rood and Test, 1968: 90–92). Area 1 comprised a mosaic of secondary habitats in a former coffee plantation, including grass, *Heliconia*, bamboo, short trees, and *Cecropia*, as well as primary cloud forest. In contrast, area 2 was mature cloud forest. There,

> the tree canopy was composed of two layers, the upper of *Gyranthera* [a tall buttressed tree in the family Malvaceae], the stilt palm *Iriartea*, and other large trees about 50 m tall and averaging some 8 m apart, while the lower included tree ferns, other palms, and small trees about 7 m high and averaging perhaps 2 m apart... the green ground cover of dwarf palms (*Geonoma*), ferns, small bushes and herbaceous plants was sparse, and the forest floor relatively open. Leaf litter was patchy... however, there were many shelters for small mammals in the form of fallen small trees and large branches, tangles of fallen small branches, large frond-like dead leaves of *Iriartea*, the bases of stilt palms, and the closely clustered aerial roots of another palm. (Rood and Test, 1968: 91–92)

The two areas showed differing patterns of capture of *Heteromys*. In area 1, trap success was highest in cloud forest and *Heliconia*, although moderate numbers of captures were also recorded in *Cecropia* and grass and a few in bamboo and secondary forest. In area 2, captures were more evenly distributed across the grid (which was entirely within cloud forest), and the trapping there yielded a higher number of unique individuals (Rood and Test 1968: 93–94).

Rood's fieldwork and observation of individuals in captivity provide some information regarding reproduction and development of *Heteromys catopterius*. Although trapping occurred only over a few weeks, the observed patterns indicated a possible peak of reproductive activity in April and May (corresponding to the onset of the rainy season; Rood, 1963: 189; see also Rood and Test, 1968: 94–96). Copulation was observed once in captivity (Rood, 1963: 189). Based on a small sample size, litter size varied from 1 to 3, and mass at birth averaged 3.3 g. Major events in the development of *H. catopterius* (measured in captivity) include: ears opened on day 5, biting (when handled) commenced on day 10, dorsal hair became apparent on day 11 (when the individuals weighed 13.7 g), walking and eating solid food began at 20 days (when individuals had full juvenal pelage, but their eyes were still closed; average weight at the time was 21.4 g), but nursing continued to day 48 (when observation ceased; Rood, 1963: 190).

Heteromys catopterius consumed a wide variety of native and exotic foods. In captivity, it ate corn especially readily but also consumed avocados, tomatoes, bread, dried cereals, rolled oats, cabbage, and cheese. The nut of the stilt palm (*Iriartea*) was found in live-traps along with *Heteromys*, presumably brought there in the animal's cheek pouches. This nut was eaten readily by captive animals, as well as several other foods found naturally in the surrounding environment: "spiny palm roots (*Bactris*), seeds and blades of an unidentified sedge, roots and blades of grasses, and fruits of *Passiflora*, the candela tree (*Gyranthera caribensis* Pittier), and several others which could not be identified" (Rood, 1963: 188). In captivity, the mice used their cheek pouches to bring corn to nest (Rood, 1963: 188–189), and while eating, "the rats did not hold the food in their front paws, as do many

other rodents, but rested it on the ground supported by the forepaws" (Rood, 1963: 189).

A few individuals were brought into captivity in the Estación Biológica and housed in elaborate experimental conditions, where nesting and digging comprised noteworthy activities. After housing individuals in cages, Rood moved some to a study room measuring 17 × 18 feet,

> prepared for the *Heteromys* in an attempt to provide conditions as similar as possible to those under which the animals lived in the wild. The floor was covered with soil to a depth of 1/2 inch. Mounds two feet deep were placed in the corners to give the animals opportunity for digging and the whole floor covered with a layer of leaf litter. One of the corners was planted with grass four feet high and another with ferns and small herbs. Palm branches were piled in the center of the room forming a brushpile. (Rood, 1963: 187)

In that environment, *Heteromys catopterius* was observed making nests and digging. Individuals

> made globular nests approximately six inches in outside diameter. In the study room where fresh and dead leaves, grass, and ferns were provided, the dead leaves were selected as nesting material and chewed into pieces four inches by two inches or smaller, which were transported in the cheek pouches. These nests were placed in the corners of the room or under the brushpile. The mice occasionally dug short tunnels in the soil banked in the room corners. Digging was done entirely with the front feet and these were used to push the loosened dirt to the surface with the palm directed outwards. (Rood, 1963: 188)

Observations by Rood also offer information regarding behavior and locomotion of the species. Adult males showed aggression toward humans, but neither adult females nor juveniles of either sex did. Adult males exhibited aggression toward females unless the latter were in estrus (Rood, 1963: 187, 191). A clear dominance structure existed, especially in the context of intraspecific competition for nests in captivity: adult males were dominant over adult females and juvenal males; and adult females over juvenal males. Dominance among adult males was determined via brief fights (Rood, 1963: 191). The mice were typically nocturnal (Rood, 1963: 188; Rood and Test, 1968: 96). Information regarding locomotion is contradictory, including the observation that individuals "run with rapid bounds and the tail does not drag" (Rood, 1963: 188) but that locomotion was "remarkably inept or phlegmatic. Their movements, mostly hops, were usually slow." (Rood and Test, 1968: 98).

For areas near Hotel Humboldt in Estado Miranda and Estado Vargas (locality 156) near the crest of the El Ávila massif of the Serranía del Litoral, field notes provide detailed ecological information for *Heteromys catopterius*. There, the species inhabits primary cloud forests, especially in association with palms. Merlin D. Tuttle and several other workers sampled this region in August and September of 1965 (see also Handley, 1976). The macrohabitat of the species at that site can be characterized as follows (M.D. Tuttle field notes, 1965):

> Primary forest... 35–65 ft [11–20 m] tall (tallest trees in stream valley), very damp with a very lush growth of moss on all the trees and vines. Many of the trees are palms 25–35 ft [8–11 m] tall which have profuse root systems about 2–3 ft [0.6–0.9 m] in diameter and 2–3 ft [0.6–0.9 m] above the ground, providing good cover. Otherwise, much of the area has fairly sparse ground cover. Bamboo is sparse to dense over the area. Along the stream, there are many mossy rocks. Ferns, moss and vines are common to the area. There are some tree ferns and many epiphytic plants. The forest is generally quite dense... dripping with moisture condensed from frequent low clouds.... The entire area is fairly dense, and there are dense-to-sparsely scattered palms over the entire area. The whole area is very wet and has usually been engulfed in dense clouds.

Furthermore, Tuttle noted that: "*Heteromys* [were] especially associated with areas of palms... some were in rock cover, and about the same number were in bamboo cover below the palm trees... [many were found] in the forest where palms were dense to at least scattered... (in contrast to *O. albigularis* [= *Nephelomys caracolus*], which seem to occur wherever there is forest)." Indeed, several species of small nonvolant mammals (but no *Heteromys*) were captured in trap lines at similar elevations in (1) forest with

bamboo understory (but few or no palms); (2) forest with disturbed understory (ferns, grass, moss, etc., but few or no palms); and (3) grassy areas.

Detailed microhabitat information for *Heteromys catopterius* at Hotel Humboldt is available as well (M.D. Tuttle field notes, 1965). The species was most commonly captured in association with palms, especially at the bases of palm trees with stiltlike root clumps: in a dense growth of palms (2 individuals); in a dense palm forest 15 ft [5 m] tall; on the ground around the palms (in a palm forest about 30 ft [9 m] tall, where there were also other species of trees that reached at least 60 ft [18 m]; (3 individuals); at the base of a palm tree (2 individuals); at the bases of palm trees in the forest; at the base of a palm tree in forest 30 ft [9 m] tall; at the base of a palm where there was a dense growth of young palms and saplings 15 ft [9 m] tall; at the bases of palm trees in the forest (there are large root masses above the ground at the bases of each palm providing good cover; 3 individuals); in the root clump of a palm tree; in the roots of a palm in dense palm forest; at the root clump base of a palm tree in the forest; at the root clump bases of palms (2 individuals); in the root clumps of palms in the forest (2 individuals).

The species was also trapped in areas with bamboo, and these areas often also contained palms (M.D. Tuttle field notes, 1965): in dense bamboo; in dense bamboo in forest; in dead leaves in bamboo about 3 ft [0.9 m] tall in forest; under rocks in grass and bamboo in forest; in a dense mixture of bamboo, vines, and ferns; in a dense mixture of bamboo, vines, and ferns in the forest; in dense bamboo beneath palms; in dead leaves and low bamboo in scattered palms; in a root clump of a palm in a dense mixture of grass and bamboo; in a dense mixture of bamboo, vines, ferns, and other plants about 4 ft [1.2 m] tall; in a dense mixture of bamboo, vines, ferns, etc., about 5 ft [1.5 m] tall in the forest; in a mixture of bamboo, vines, ferns, and young palms in the dense forest; in mixture of bamboo, vines, ferns, and young palms about 6 ft [1.8 m] tall in forest of scattered palms mixed with other trees.

The species was occasionally found associated with rocks or logs, but only rarely in grass or other microhabitats (M.D. Tuttle field notes, 1965): in rocks; in rocks in the forest; under a rock in dense forest; on mossy rocks in the forest (3 individuals); under large mossy rocks in the forest near the stream; under fallen trees (2 individuals); in a hollow tree in dense forest; on the trunk of a leaning tree in dense forest 45 ft [14 m] tall; on a dead log 8 ft [2.4 m] above the stream and spanning a distance of 25 ft [8 m] from one side to the other, on one side there was dense bamboo, and on the other a mixture of dense ferns and young bamboo (the forest above was up to 60 ft [18 m] tall); in dense grass a short distance from the palm forest; in dense grass about 1.5 ft (0.5 m) tall near the stream in a slightly open part of the forest; in dense vines 6 ft (1.8 m) from the stream; at the entrance to a hole under a root ledge.

At Hotel Humboldt, the species only occasionally was recorded to have held items in its cheek pouches (M.D. Tuttle field notes, 1965). Two individuals were taken carrying palm nuts 26 × 22 mm in their pouches. Each had one nut, and one of them also had half a millipede in its pouch with the nut. A third individual had a palm nut 27 × 20 mm in its pouch.

Further information regarding the natural history of *Heteromys catopterius* derives from the results of surveys conducted in the Río Morón drainage on the northern slopes of the Cordillera de la Costa in Estado Carabobo. Francisco J. Bisbal-E. and colleagues (Sergio Bermúdez, José Daniel P. Bora, Arnaldo Ferrer, Alfredo Lander, Alejo Ospino, and Ramón Rivero) undertook a general inventory of vertebrates in the Río Morón drainage in 1990–1991, including trapping for small nonvolant mammals (Bisbal-E., 1993). Much of the region had been cultivated for many years, but in 1971 an effort began to return the area to a more natural state for the purpose of restoring water supply to small towns and a large industrial complex on the coast. Although not all captured individuals were collected, all the voucher specimens of *Heteromys* that we have examined from this work represent *H. catopterius* (from La Justa and Palmichal; appendix 1). *Heteromys catopterius* was one of the most commonly captured species in both cloud forest and semideciduous forest in

this area, and it inhabited some secondary areas in addition to primary forest (Bisbal-E., 1993).

At La Justa (300–400 m; locality 141), *Heteromys catopterius* and *Proechimys guairae* were the most commonly captured small, nonvolant mammals. The macrohabitat at La Justa was recovering semideciduous forest. The area had been cultivated for coffee, cocoa, and other crops for many years, but the croplands had been abandoned, leading to the formation of secondary forest before the inventory work commenced. The forest had a "fairly dense but irregularly distributed shrub layer, due to differing light conditions within the forest, and [overall, the forest had] two or three dense strata with an average height of 15–20 m" (Bisbal-E., 1993: 366; translation ours).

At Palmichal (700–1000 m; localities 143 and 144), *Heteromys catopterius* and *Oryzomys albigularis* (= *Nephelomys caracolus*) constituted the most commonly captured small, nonvolant mammals. The macrohabitats at Palmichal included both primary and secondary cloud forests. The latter were abandoned coffee plantations and small plots of subsistence agriculture that had regrown by the time of the inventories. The cloud forest "has an average height of 20–25 m with emergent trees reaching 30–40 m; it has 2–3 strata and a well-developed understory. Epiphytes are abundant on higher branches and treetops, whereas lianas are rare" (Bisbal-E., 1993: 366; translation ours). At both La Justa and Palmichal, *H. catopterius* was captured only on the ground, despite the placement of traps on tree branches as well.

Sympatry and Zones of Contact with *Heteromys anomalus*: Presently available specimens indicate that *Heteromys catopterius* and *H. anomalus* show largely complementary distributions in north-central and northeastern Venezuela. Apparently, the distributions of the two species are generally parapatric, with only very narrow zones of sympatry. In general, *H. catopterius* inhabits higher, wetter areas than *H. anomalus*. Known sites of contact between the species occur in the Rancho Grande region in the western portion of the Serranía del Litoral, the El Ávila massif of the Serranía del Litoral, the Tiara region of the Serranía del Interior, and the Caripe region of the Macizo Oriental (figs. 1, 4). Similar parapatric distributions have been observed for several other pairs of species in the subfamily (Genoways, 1973; Rogers and Engstrom, 1992; Anderson, 1999; Anderson and Jarrín-V., 2002; Anderson and Timm, 2006).

The most detailed distributional information for an area of geographic contact between *Heteromys catopterius* and *H. anomalus* derives from the Rancho Grande region (in the western portion of the Serranía del Litoral). There, the distributions of the two species meet on both the southern and northern slopes. On the southern slope, the species' distributions come into contact at ca. 1050 m. Many specimens of *H. catopterius* from the Rancho Grande region correspond to areas near the Estación Biológica de Rancho Grande and El Portachuelo. El Portachuelo (locality 136) lies at the crest of the range and represents a pass between Pico Periquito and Pico Guacamaya. The Estación Biológica (localities 47 and 137) lies on the southern slope, slightly higher than and just to the east of El Portachuelo. Near the Estación Biológica and El Portachelo, *H. catopterius* was captured in large numbers in cloud forests and secondary forests (see Natural History; C.O. Handley, Jr. field notes, 1960). In contrast, only a few specimens of *H. anomalus* exist from areas near the Estación Biológica. One was collected by William Beebe; it was taken in an unspecified habitat within 1 km of the Estación Biológica (Tate, 1947). The Smithsonian Venezuelan Project collected three *H. anomalus* from areas slightly below the Estación Biológica on the southern slope; most of the sampling was in secondary habitats, especially in and near a "banana grove with thick underbrush and tall tress" (N.E. Peterson field notes, 1965). The tags for those specimens indicate that one was captured "in dense herbs—coffee and banana growth" and the other two in "dense herbs and banana plants." In addition, the Smithsonian Venezuelan Project also collected an individual (USNM 371016) that shows a mixture of morphological characters of the two species and may represent a hybrid between them. We provisionally identify it as *H. catopterius*, but genetic studies are necessary to examine the

possibility of limited hybridization between the two species in this region intimated by the morphological data. This specimen derives from the same macrohabitat as the three individuals of *H. anomalus*, and the tag indicates the microhabitat as at the "base of sapling, low herbs." Interestingly, *H. catopterius* was captured in an area *below* the Estación Biológica on the southern slope along a stream in rainforest habitat (habitat described and pictured in Voss, 1988: 417–420; R.S. Voss field notes, 1979). Taken together, the available natural history information suggests that the two species likely segregate by habitat type (*H. catopterius* in wetter and/or more mature habitats and *H. anomalus* in drier and/or more disturbed areas) at a local scale in this area.

Records also document the presence of both species from the northern slope of the Serranía del Litoral just north of El Portachuelo and Rancho Grande. Researchers from the Museo del Instituto de Zoología Agrícola (Universidad Central de Venezuela) in Maracay surveyed small mammals at many elevations along the highway that passes by Rancho Grande and leads to Ocumare de la Costa. Both *Heteromys catopterius* and *H. anomalus* have been documented from 900–920 m on the northern slope (localities 45 and 130); in addition, *H. anomalus* is known from 630 m (locality 44), and *H. catopterius* from 680 m (locality 129). No habitat information accompanies these records.

Additionally, two sites of sympatry and one site of near parapatry exist in the central portion of the range of *Heteromys catopterius*. The two species come into geographic contact on the northern slopes of the El Ávila massif (in the central portion of the Serranía del Litoral). There, both species have been collected in very large numbers at Los Canales de Naiguatá, at 720–800 m (localities 120 and 160; see Valdez et al., 1985). Because these water-gathering canals span several kilometers, it is not clear whether or not the species coexist in the same macrohabitat or, alternatively, are separated by habitat and/or elevation. Specimens also document an area of geographic contact between the two species in the Tiara region of the Serranía del Interior. The species are sympatric at Campamento Rafael Rangel (= Loma de Hierro/Minas de Niquel; localities 53 and 138) at 1260 m, but no habitat information exists for any of the specimens. *Heteromys catopterius* exists from 1200 m at the same site, and *H. anomalus* occurs at nearby localities of La Horqueta (locality 51) and Agua Amarilla (locality 52), at slightly lower elevations (ca. 1080–1100 m). At the eastern end of the main Aragua-Carabobo chain of the Serranía del Litoral, the two species come into close geographic contact, although no known site of sympatry exists. Here, *H. catopterius* inhabits El Laurel (locality 155) at 1355 m, and *H. anomalus* occurs at the nearby sites Turgua (1144 m; locality 76) and Bosquecillo, on the campus of the Universidad Simón Bolívar (ca. 1100 m; locality 75).

Finally, the two species come into geographic contact in the Caripe region of the Macizo Oriental. There, two very nearby sites of sympatry exist: La Laguna (1330 m for *Heteromys anomalus* and 1170–1335 m for *H. catopterius*; localities 84 and 159 for *H. catopterius*) and an area sampled near San Agustín (1180–1260 m for *H. anomalus* and 1170–1180 m for *H. catopterius*; localities 84 and 159). In addition, *H. catopterius* occurs at two nearby sites (San Agustín, 1270 m and Hacienda San Fernardo, 1320 m; localities 157 and 158), and closeby, *H. anomalus* is known from the Cueva del Guácharo (1060–1065 m; locality 86). Finally, two specimens (USNM 409820 and 409821) from Cueva del Guácharo (1010 m) display a mixture of characters of the two species; although provisionally we ascribe them to *H. anomalus*, they may constitute rare hybrids between the two species. Future genetic studies in the region are necessary to address this possibility. In contrast to the well-documented area of contact between the two species in the region of Rancho Grande (see above), the few available records from near Caripe do not allow for any clear characterization of habitat-related, successional, and/or elevational separation between the two species.

CONSERVATION STATUS: *Heteromys catopterius* probably faces minimal risk of extinction or even population-level decline in most of its range. Like most species of the genus, data available from field collectors indicate that the species inhabits only closed-canopy evergreen forests (i.e., not deciduous

forests, xerophytic vegetation, natural grasslands, or open agricultural areas). Among the evergreen montane forests it inhabits, the species appears especially associated with cloud forests and with areas holding an abundance of palms. Fortunately, it shows substantial tolerance for disturbance within forested ecosystems. In addition to particularly frequent collection in mature cloud forests, the species also has been trapped in large numbers in secondary forests (e.g., at Rancho Grande; see Natural History). In addition, *H. catopterius* exhibits a moderately widespread distribution (throughout most of the Cordillera de la Costa). Finally, many national parks and other governmentally protected reserves harbor known localities of the species: Parques Nacionales El Ávila, El Guácharo, Henri Pittier, Macarao, Miguel José en Sanz San Esteban; and Monumentos Naturales Cueva del Guácharo and Pico Codazzi). *Heteromys catopterius* also has been documented from private lands conserved as a natural watershed in the Río Morón drainage (Bisbal-E., 1993). The protection afforded these reserves varies greatly, but large areas of intact forest remain in several of them (perhaps most notably the Parque Nacional Henri Pittier and Parque Nacional El Ávila).

Heteromys anomalus (Thompson, 1815)
Caribbean Spiny Pocket Mouse

DISTRIBUTION: Distributed across much of northern Colombia and Venezuela and in the upper Río Magdalena Valley of central Colombia, from near sea level to middle elevations; also inhabits the nearby Caribbean islands of Margarita, Trinidad, and Tobago (figs. 1, 4; Anderson, 2003b; appendices 1 and 2). In addition to regions dominated by forest, *H. anomalus* also inhabits restricted forested areas (riparian gallery forests) in the *llanos* (savanna) of Venezuela (August, 1984; Soriano and Clulow, 1988). The species typically ranges from sea level to ca. 1600 m in elevation, although its upper distributional limit is lower in some mountain ranges (e.g., the Cordillera de la Costa in Venezuela; see Biogeography of *Heteromys catopterius* and *H. anomalus*); a population in the semi-isolated Macizo de Guaramacal in western Venezuela inhabits an anomalously high elevation (2430 m; Anderson, 2003b). Note also seven localities of *H. anomalus* in the central and western *llanos* of Venezuela reported by Utrera et al. (2000); we have examined vouchers only from one of those sites (Caño Hondo, locality 66, appendix 1); the remainder probably represent new records of *H. anomalus*.

DIAGNOSIS: A species of spiny pocket mouse with adults showing the following combination of characters (figs. 6, 7, 9): p4 (lower permanent premolar) with three lophids; P4 (permanent upper premolar) with straight, moderately long fold in anterior margin of posterior loph; tubercle or swelling at posteroventral border of infraorbital foramen absent; mesopterygoid fossa formed by long, thin hamular processes of pterygoids; optic foramen especially small, with posterior margin formed by strong bar of bone; parietomastoid suture dipping well ventral to parietal crest posterior to its widest point, then ascending dorsally to rejoin crest near its posterior termination; rostrum moderately long and generally moderately tapered anteriorly, without anterodorsal flare; anterior portion of premaxillary convex (inflated), forming a smooth (not stepped) lateral border of rostrum; interorbital constriction narrow; braincase narrow and not inflated; interparietal variable in size and shape; skull average for genus (ONL 31.06–39.02 mm in adult specimens of age class 4; table 1, appendix 3); dorsal pelage typically pale brown strongly grizzled with thin ochraceous hairs intermixed among spines, but occasionally almost uniformly dark drab gray (in wet lowlands of Estado Zulia, in some parts of the Cordillera de Mérida, in mesic areas of Estado Monagas and Estado Sucre, and on the island of Tobago), usually harsh and spiny, but often softer in montane regions; weak patch of dark coloration present on dorsal and external surfaces of forearms, continuous with dark coloration of flanks; ears distinctively rounded, brown to gray and large relative to body size; orange band on flanks absent; tail typically strongly bicolored and slightly to moderately longer than head-and-body length; plantar surface of hind feet naked.

KARYOLOGY: Engstrom et al. (1987) reported the standard karyotype of 2n = 60,

FN = 68 for 20 individuals of *H. anomalus* from Estado Miranda (24 km N Altagracia de Orituco and 25 km N Altagracia de Orituco, localities 79 and 80), Estado Monagas (Caripito, locality 88) and Estado Sucre (40 km SW Caripito, locality 104), with voucher specimens deposited at the TCWC and CM. Although those authors did not provide museum catalog numbers for the specimens that were karyotyped, we have examined specimens from three of these localities in those museum collections (appendix 1); all represent *H. anomalus*.

COMPARISONS: See above for comparisons with *Heteromys catopterius*, and Anderson (2003b) and Anderson and Timm (2006) for comparisons with other species of the genus.

GEOGRAPHIC VARIATION: Although a comprehensive review of geographic variation in the widespread *Heteromys anomalus* lies beyond the scope of the current work, some noteworthy patterns exist. Externally, a few populations in mesic areas (e.g., wet regions of Estados Lara, Monagas, Sucre, and Zulia in Venezuela, and on the island of Tobago) show darker, less grizzled dorsal pelage than populations in most parts of the species' range (see also Anderson, 2003b). One doubly insular population (Bush Bush Forest; locality 22) exhibits markedly smaller size than other examined populations (Anderson, 2003b). It corresponds to the tiny island of the same name, which lies within the Nariva Swamp in central-eastern Trinidad (Downs et al., 1968).

NATURAL HISTORY: Field notes and published studies provide substantial ecological information on *Heteromys anomalus* from a few sites where it was collected in large numbers in eastern Venezuela and Trinidad and Tobago. However, as mentioned above (see account of *H. catopterius*), the extensive information provided by Valdez et al. (1985) for the genus at Los Canales de Naiguatá in Estado Vargas in the Serranía del Litoral corresponds to pooled data for *H. anomalus* and *H. catopterius* (localities 120 and 160; appendix 1); we do not include natural history information from that site here. See Anderson (2003b) for summaries of natural history information for sites in Colombia and western Venezuela.

On the slopes of the Macizo Oriental (fig. 1) in Estado Monagas and Estado Sucre, field notes indicate that *Heteromys anomalus* was captured commonly in intact tropical rainforest adjacent to cropland but only occasionally in drier areas more dominated by agriculture. G.H.H. Tate and H.J. Clement sampled several sites in this region in March–May 1925 (see also Tate, 1931). The area at Neverí (locality 111) where *H. anomalus* was common, was:

> entirely covered with splendid forest, and although dry at present, I judge that it has a very severe rainy season from the luxuriance of its clothing of vegetation. It is only within the last few years indeed that a road has been made into the headwaters of the Neverí, and as yet clearings are not plentiful.... [Along the river] runways are plentiful, and the river-banks have a moderate slope, and are studded with large boulders, over-topped by giant forest and buried in a rich growth of *platanillos*. Toward the upper part of the line the banks become rather steeper, slatey outcroppings protruding their faces into the water-way... in steaming, rotting jungle.... [A] very abundant plant in the forest is a slender-stemmed moderately tall palm, which has its trunk quite clothed with long stiff, needle-pointed spines.... 'Elephant-ears' and great arboreal aroids are plentiful. (G.H.H. Tate field notes, 1925)

Latal (locality 113), another site where *H. anomalus* was common, "is surrounded by high hills all partly cleared in their lower slopes and planted to coffee. However there is much fine forest." (G.H.H. Tate field notes, 1925).

In contrast, *Heteromys anomalus* was captured only occasionally by Tate and Clement at San Antonio de Maturín (locality 89), a drier region with denser human settlement. The region as a whole holds "xerophytic vegetation, but far up the valley on either hand one can descry good looking forest." (G.H.H. Tate field notes, 1925). The valley floor was densely populated, and many pastures were present. The valley was drained by "a stony, broad, shallow stream meandering between alternate small bluffs and *playas*. Along this stream are also large stands of *caña lata*, the tall reed-like cane often used for walling in native houses where no strength is needed" (G.H.H. Tate field notes, 1925).

At Finca Vuelta Larga (locality 101) in the lowlands of Estado Sucre, field notes indicate that *Heteromys anomalus* was captured in areas of secondary evergreen forest as well as adjacent small agricultural plots, but not in inundated savannas of grasses and sparse shrubs. Robert S. Voss, Hernán C. Castellanos, and Carlos Gauveca-C. sampled these managed and seminatural habitats in August 1987 (R.S. Voss and H.C. Castellanos field notes, 1987; see also Voss, 1991). The area comprised a mosaic of inundated savannas (*estero*) and secondary forests (*mato*) at slightly higher elevations. Similar numbers of traps were set in inundated savanna and in forest, as well as a lesser number in small recently established agricultural plots (*conuco*). The savanna was flooded by use of a series of dikes and fenced for heavy grazing; shrubs and tall herbs grew along the fences, where most of the savanna traps were set. The forest was secondary growth, cleared ca. 14 years prior for small agricultural plots and allowed to regrow (abandoned *conuco*). The vegetation there was "a dense tangle of second-growth trees (mostly unbuttressed) and shrubs with many viny tangles" (R.S. Voss field notes, 1987). This secondary forest was evergreen and dominated by palms, with a variable and discontinuous canopy ca. 30 m high (H.C. Castellanos field notes, 1987). *Heteromys anomalus* was captured in secondary forest and recently established agricultural plots (*conuco*) but not in traps set in the wet, marshy savanna margins under fences, tall grass, and occasional shrubs.

Some information regarding the microhabitats of *Heteromys anomalus* at Finca Vuelta Larga is also available (R.S. Voss, H.C. Castellanos, and C. Gauveca-C. field notes, 1987; translations ours, where relevant): on the ground in leaf litter under dense undergrowth in forest; on bare ground under tangled lianas with leaf litter on top, and under stilt roots of a *Cecropia*; on ground in wet leaf litter under tall grass in old [abandoned] *conuco* (grass, bushes, plantains, and small trees); on ground in leaf litter and below a group of lianas that surround a palm (*Corozo*) 665 mm in dbh; on ground in tall grasses and shrubs (2 individuals).

The species may be an agricultural pest in at least some regions. In the original description, Thompson (1815) noted that "The habits of this tribe of rats are singular and curious: where numerous, they do incalculable mischief in barns and granaries; for, not satisfied with what they can eat on the spot, they stow away and carry off in their cheek pouches no inconsiderable quantity [of grain], to be deposited in their retreats for times when food is not to be procured from without" (Thompson, 1815: 162). We know of no studies quantifying the extraction of agricultural grain by *Heteromys anomalus*. Whereas the species does not inhabit large fields of mechanized agriculture (see Utrera et al., 2000; Anderson, 2003b), it does exist in many areas containing smaller fields in subsistence agriculture settings (see above), where it may be a pest to humans.

Substantial natural history information exists for *Heteromys anomalus* at a site in Trinidad where large numbers of the species were captured during surveys that spanned several years. Teams from the Trinidad Regional Virus Laboratory surveyed Bush Bush Forest (locality 22) for small, nonvolant mammals from 1960–1963 (Worth et al., 1968; see also Aitken et al., 1968). Downs et al. (1968) provide detailed information on the region, which we summarize here. Bush Bush Forest is the name given to the areas sampled on Bush Bush Island, a low, forested island present in the Nariva Swamp of central-eastern Trinidad. The island has sandy, well-drained soils and is approximately 0.25 mi (0.40 km) wide and 2–3 mi (3–5 km) long. Although most of the island itself is never flooded, it merges into areas that are seasonally inundated that support swamp forest comprised of palms and a few hardwoods. Most of the surrounding open swamp, however, is almost continuously inundated, covered by grass, cane, or aeroids. Before 1960, the island received only periodic visits by humans for fishing during the dry season, as well as sporadic visitation associated with hunting or selective extraction of timber. Both removal trapping and mark-recapture studies were undertaken; all voucher specimens that we examined from this work represent *H. anomalus* (appendix 1).

Heteromys anomalus was consistently one of the most commonly collected small, nonvolant mammals in nonflooded forested

areas on Bush Bush Forest, and a variety of information regarding its natural history is available (Worth et al., 1968, from which the following information derives). Removal trapping spread over several parts of the island over four years yielded a total of 423 individuals of *H. anomalus*, with an overall trap success that varied from 0.3 % to 2.5 % in individual years. A general decline in numbers was observed during the study. Minimal trapping in swampy habitats failed to capture any *Heteromys*. Mark–recapture studies in the Restan area of Bush Bush Island captured 183 individuals (including recaptures) over three years, with much higher trap success (8.2%). The species showed a small home range, "rarely entering traps in more than two adjacent stations" that were set an average of ca. 100 ft (30 m) apart (Worth et al., 1968: 271). No individual of the species was found to have moved even 300 ft (91 m). Immature individuals were present in every month of the year but January, but were most frequent from May through October (the wet season). Some individuals were followed for more than six months. The species "tended to begin foraging earlier in the evening than other species" (of rodents and marsupials; Worth et al., 1968: 271).

Some behavioral information in captivity is available for individuals of *Heteromys anomalus* from the island of Trinidad. John F. Eisenberg conducted a landmark comparative study of behavior across the family Heteromyidae (Eisenberg, 1963). Most of his investigation of the genus *Heteromys* focused on *H. lepturus* (from Finca La Selva, Veracruz, Mexico; = *H. desmarestianus*; see Anderson et al., 2006, for geographic variation within the *H. desmarestianus* complex). In addition, however, four individuals of *H. anomalus* were surveyed for individual behavior and some aspects of intraspecific social behavior. These individuals were provided by the Trinidad Regional Virus Laboratories from an unspecified location, presumably in Trinidad. Individuals were held in terraria at high humidity with soil covering the floor. Observations were performed at night using a red light for illumination. In male-female encounters, *H. anomalus* was less aggressive than species of other heteromyine genera, with "chasing" constituting the primary aggressive behavior of *H. anomalus* (Eisenberg, 1963: 50, see also 68, 94). Both naso-nasal and naso-anal behaviors were observed between individuals of the opposite sex (Eisenberg, 1963: 51–52). Subsequently, preliminary sexual behaviors were observed, but copulation was not: "Driving [chasing and attempting to mount the female], perineal investigation, grooming, patting, and mounting [gripping of flanks of female with forelimbs, pressing ventrum against back of female and attempting intromission] were displayed by the males. A typical lordosis [freezing movement, allowing the male to mount as the female raises her hindquarters] was shown by the females.... The male *Heteromys* [*anomalus*] uses a neck grip [grasping with incisors the fur over the dorsal gland of the female during a mount]" (Eisenberg, 1963: 51, see also 47, 58).

On the island of Tobago, field notes document the capture of *Heteromys anomalus* near Charlottesville on the slopes of Pigeon Peak in several forested habitats (especially montane forest) but not in areas under active cultivation (locality 1; R.S. Voss and M.E. Holden field notes, 1989). Robert S. Voss and Mary Ellen Holden sampled a variety of habitats in this region in January 1989 (see also habitat descriptions and photographs in Voss, 1991: 73–76). *Heteromys anomalus* was the most commonly captured small nonvolant mammal in montane forests, whereas *Zygodontomys brevicauda* was the most common in most other sampled habitats. *Heteromys anomalus* was also captured occasionally in lowland primary rainforest (Voss, 1991) and abandoned cocoa plantations with an intact original canopy. The species was not caught in agricultural clearings (cocoa, plantains, pigeon peas, papaya, and cassava [manioc]) or in active cocoa plantations (R.S. Voss field notes, 1989). The montane forest where *H. anomalus* was especially common can be characterized as follows:

> This mature... forest is developed along the main ridge above about 1500 ft [457 m] elevations.... This part of the ridge is probably cloud-covered at least briefly on most days and so the vegetation is very wet and has a montane aspect despite the insignificant altitude. Physi-

> ognomically, this ridge-top forest at only 1600 ft [487 m] elevation has the appearance of Andean forests found at much higher elevations.... The forest along the ridge-top... is not very tall, the canopy only about 25–30 m or so, or even less in areas more exposed to the wind. The trees that form the canopy are also of much lesser girth than in lowland forests and are seldom buttressed.... Small, graceful *Euterpe* palms are much more abundant in these forests than below and often emerge into the canopy. The undergrowth is denser here than in lowland forests and includes seedling trees and woody shrubs as below, but large ferns and Cyclanthaceae are commonest. Gingers and *Heliconia* are present too. Small tree-ferns are common in a few situations. Many of the tree trunks support dense growths of climbing aroids and cyclanths, and orchids and bromeliads are abundant even near ground level. Many tree trunks are mossy, but the moss is a thin film and does not form thick, wet mats. Tangled vines (including some woody lianas) are common everywhere. The forest floor is thickly littered with leaves, twigs and branches and scattered with fallen logs. There is a thin humus layer over the clay in some places. (R.S. Voss field notes, 1989)

Information regarding the microhabitats of *Heteromys anomalus* near Charlottesville is also available (R.S. Voss and M.E. Holden field notes, 1989). All were captured on the ground in forest (all but four in montane forest). Individual microhabitats follow: under fallen vegetative litter and leaves; under wet vegetative litter and leaves beside tree; under fallen palm fronds; under rotting palm fronds beside large tree; beside rotting log under dead palm frond, fallen branches and other vegetative litter; under log; under inclined tree trunk (2 individuals); under roots of fallen tree; under stilt roots of *Cecropia*; under stilt roots of small tree; under tree ferns and aroids; beside trees under tangled vines; beside buttress of large tree with vine coverage.

Conservation Status: *Heteromys anomalus* faces no substantial risk of extinction, but local populations are vulnerable to declines or extirpation in areas undergoing deforestation. Available data indicate that *H. anomalus* inhabits principally closed-canopy forests, but not xerophytic vegetation, natural or anthropogenic grasslands, or large, open agricultural areas (e.g., mechanized agriculture; Utrera et al., 2000). However, in contrast to most species of the genus, it is also known from small plots of subsistence agriculture; see Natural History; see also Anderson, 2003b: 24–25). Furthermore, in addition to evergreen forests typical of the genus, it also inhabits areas where deciduous forests constitute the predominant vegetational type. In such regions, however, it remains unclear whether the species occupies deciduous forests per se, or only smaller areas of evergreen vegetation in more mesic situations, such as along watercourses. The species exhibits a very widespread distribution throughout most of northern Colombia and northern Venezuela, as well as much of Trinidad and Tobago. In central and eastern Venezuela, the species has been collected in many national parks (Parques Nacionales Cerro El Copey-Jóvito Villalba, El Ávila, El Guácharo, Guatopo, Henri Pittier, Miguel José en Sanz San Esteban, and Península de Paria) and other governmentally protected areas (Monumentos Naturales Cerros Matasiete-Guayamurú and Cueva del Guácharo). These reserves receive varying levels of protection; whereas some face substantial human pressure, others (e.g., Parque Nacional Henri Pittier) contain large extents of intact forest.

DISCUSSION

Biogeography of *Heteromys catopterius* and *H. anomalus*

Endemism in the Cordillera de la Costa: Current information suggests that *Heteromys catopterius* is endemic to the Cordillera de la Costa (figs. 1, 4). Records derive from throughout the Serranía del Litoral, and the species is also known from one area of the Serranía del Interior (near Tiara, in Estado Aragua). Because this latter range is lower and drier, it probably offers much less extensive areas of suitable habitat for the species. *Heteromys catopterius* is not known from mountain ranges to the west of the Cordillera de la Costa. No records of the species exist in the Sierra de Aroa to the west of the Cordillera de la Costa and separated from it by the Depresión de Yaracuy

(SAGCN, 1995). The floral composition of the Sierra de Aroa shows strong similarities to the Cordillera de la Costa (Huber, 1997), but the upper portions of that range have received very little sampling by mammalogists, and conclusions regarding its mammalian fauna must await further fieldwork (see Anderson, 2003a, for methods of testing hypotheses regarding a species' absence). The presence of *H. catopterius* seems much less likely in the Cordillera de Mérida or Serranía de San Luis even farther to the west. Extensive sampling for small nonvolant mammals has occurred in many portions of the Cordillera de Mérida, yielding many records of *H. anomalus* (Anderson, 2003b). The Serranía de San Luis occupies a very isolated position far from other mesic montane regions in northern Venezuela, and available records document the presence of *H. anomalus* there as well (Anderson, 2003b).

Similarly, several mountain ranges present near the eastern end of the known distribution of *Heteromys catopterius* lack records of the species. Two subranges comprise the Macizo Oriental (the easternmost portion of the Cordillera de la Costa). All documented populations of *H. catopterius* in the Macizo Oriental correspond to the Caripe region in the eastern subrange, which is lower and wetter (Huber, 1997). None derive from the higher and drier Cerro Turimiquire subrange just to the west, an area that has received little sampling by mammalogists (Tate, 1931; G.H.H. Tate field notes, 1925). The only specimen of *Heteromys* known from the higher areas on Cerro Turimiquire represents *H. anomalus* (locality 114). Similarly, no records of *H. catopterius* exist from moderately high montane regions on the Península de Paria in extreme northeastern Venezuela, where *H. anomalus* is known, or on Trinidad or Tobago, two continental islands with plentiful records of *H. anomalus*. Interestingly, the habitat of *H. anomalus* at Pigeon Peak in Tobago (see Natural History of *H. anomalus*) holds many similarities with that of sites on the mainland where *H. catopterius* has been collected in large numbers (e.g., Rancho Grande and Hotel Humboldt; see Natural History of *H. catopterius*).

Following current taxonomy, the Cordillera de la Costa harbors only three endemic species of mammals, out of the 327 (Linares, 1998) to 351 (Ochoa-G. and Aguilera-M., 2003) mammals estimated to inhabit Venezuela. An oryzomyine rodent, *Nephelomys caracolus* (formerly included in the *Oryzomys albigularis* species complex) shows a distribution somewhat similar to that of *Heteromys catopterius*, inhabiting the central portion of the Cordillera de la Costa (both the main Aragua-Carabobo chain and the El Ávila massif) at elevations between 1050 and 2300 m; however, in contrast to *H. catopterius*, no records of *N. caracolus* exist from the Serranía del Interior or the Macizo Oriental (Percequillo, 2003; see also Aguilera et al., 1995a; Márquez et al. 2000; Anderson, 2003a). Even more restricted, an ichthyomyine rodent, *Ichthyomys pittieri*, remains known from only a few specimens from the Serranía del Litoral (Handley and Mondolfi, 1963; Voss, 1988). Whereas several species of nonmammalian tetrapods show distributions restricted to montane areas on the Península de Paria in northeastern Venezuela (Estado Sucre) as well as in the Cordillera de la Costa (see below), currently available information indicates that no mammal shows that pattern. Not surprisingly, the mammals endemic to the Cordillera de la Costa are rodents, which typically show small home ranges and low dispersal abilities. Future taxonomic revisions may alter this preliminary information by bringing to light other endemic species currently considered to belong to widespread species (as has happened with revisions of the common rodents *Heteromys* and *Nephelomys*). On the contrary, however, new fieldwork may extend the known ranges of these three species, altering the present conclusions regarding their endemism.

Rates of avian endemism in the Cordillera de la Costa appear grossly similar to the situation in mammals, but estimates range much higher for amphibians and reptiles. Although taxonomic studies and inventory work remain incomplete (especially for amphibians and reptiles), we provide information from available biogeographic summaries of nonmammalian tetrapods (note that regions of endemism in Cracraft [1985] and Péfaur and Rivero [2000] include the surrounding lowlands; therefore, the information provided in those sources cannot be used

in the present comparisons of *montane* endemism). Among a total of 1360 species of birds considered to occur in Venezuela, seven or eight are endemic to the Cordillera de la Costa (Lentino-R., 2003); broadening the definition of the region of endemism to include montane areas on the Península de Paria would add five other species. Note, however, that Hilty (2003) indicated more extensive distributions for five of these 13 species, including other montane systems in northern Venezuela, most commonly the Sierra de Aroa and Serranía de San Luis. Of the 284 species of amphibians documented for the country, 27 are endemic to a region including the Cordillera de la Costa and the Península de Paria; information for amphibian endemism in the Cordillera de la Costa itself is not available (La Marca, 2003a). In total, 341 species of reptiles are estimated to inhabit Venezuela, but published information regarding Venezuelan reptiles in the Cordillera de la Costa remains lacking (La Marca, 2003b). Ongoing research indicates that at least 27 species of reptiles are endemic to the Cordillera de la Costa and montane areas on the Península de Paria; at least 20 of those are endemic to the Cordillera de la Costa itself (G. Rivas, in litt.). As is the case for mammals, future fieldwork and taxonomic research may alter these conclusions.

ECOGEOGRAPHY: Although most localities of *Heteromys catopterius* correspond to wet highland sites (including many cloud forests), the species also has been documented at intermediate elevations in sufficiently wet areas. The lowest occurrence record of the species on the southern versant of the main Aragua-Carabobo chain lies at 1050 m (Rancho Grande; locality 137), but the species inhabits wet forests at 680 m elevation on the moister northern slope in Estado Aragua (Carretera Estación Biológica Rancho Grande–Cata, km 29; locality 129) and even as low as 350 m in the Río Morón drainage in Estado Carabobo (La Justa; locality 141; figs. 1, 4). On the El Ávila massif, the species descends to 1050 m on the southern slope along the border between Distrito Captial and Estado Miranda (Quebrada Chacaito; locality 147), but records of the species are known from as low as 720 m on the wetter northern slope (Los Canales de Naiguatá; locality 160; Estado Vargas). These altitudinal patterns coincide with known vegetational differences. Although much local variation exists (related to factors such as exposure to wind), mesic vegetational zones generally descend farther on the northern (Caribbean-facing) slope of the Serranía del Litoral than on the southern, interior versant (Huber, 1997; Ataroff-S., 2003; Meier, 2004).

We conclude that *Heteromys catopterius* has a disjunct distribution within the Cordillera de la Costa. At the very least, the low, dry Depresión de Unare surely isolates the eastern populations in the Macizo Oriental from those in the western and central part of the range of the species. In addition, the central populations on the El Ávila massif may be disjunct from the western populations in the main Aragua-Carabobo chain, due to the drier and moderately low saddle drained by the Quebrada Tacagua on the northwest and the Río Guaire on the southeast (through the city of Caracas). It remains even less clear whether populations in the Serranía del Interior are contiguous with those of the Serranía del Litoral. In any case, the species constitutes a system propitious for fascinating phylogeographic work, especially in a comparative context (i.e., in comparison with other codistributed species, such as *Nephelomys caracolus*) and in conjunction with niche-based distributional modeling in a Geographic Information Systems (GIS) framework (Graham et al., 2004; Phillips et al., 2006).

The ecogeographic patterns of records of *Heteromys anomalus* also merit comment and future research. *Heteromys anomalus* only rarely inhabits localities over 1400 m in regions of the Cordillera de la Costa where *H. catopterius* is present. *Heteromys anomalus* shows a distribution complementary to that of *H. catopterius*, inhabiting higher elevations on the southern (interior) slopes of the central portions of the Cordillera de la Costa than it does on the northern versants. Eight localities above 1000 m exist for *H. anomalus* in the central portion of the Cordillera de la Costa, but none reaches 1400 m (localities 47, 51–53, 62, 63, 75, and 76, Estados Aragua, Carabobo, and Miran-

da, 1050–1350 m). All pertain to either the southern slopes of main Aragua-Carabobo chain or the Serranía del Interior. In contrast, the highest records of the species on the northern slope of the main Aragua-Carabobo chain and the El Ávila massif are only 920 m and 800 m, respectively (locality 45, Estado Aragua; locality 120, Estado Vargas). In the eastern portion of the Cordillera de la Costa (the Macizo Oriental), *H. anomalus* occurs at elevations above 1000 m at five localities. Four lie in the eastern portion of the Macizo near Caripe and known records of *H. catopterius*, and only one of those corresponds to an elevation above 1400 m (localities 82–84, 86, Estado Monagas, 1060–1550 m). The last is from Cerro Turimiquire at a much higher elevation (locality 114, Estado Sucre, 6000 ft [1829 m]) in the western portion of the Macizo, which is drier (Huber, 1997) and where no record of *H. catopterius* is known.

In contrast to its distribution in the Cordillera de la Costa (where it very rarely exceeds 1400 m), *Heteromys anomalus* is documented from localities above 1400 m in several ranges to the west, outside the range of *H. catopterius*. These include the Sierra Nevada de Santa Marta (San Miguel, Departamento de La Guajira, Colombia, 1700 m), Serranía de Perijá (Sierra Negra, Departamento de la Guajira, Colombia, 1500 m), Serranía de San Luis (Cerro La Danta, Estado Falcón, 1300–1470 m), and Cordillera de Mérida (Cerro Alto, Estado Barinas, 1460–1600 m; El Blanquito and other localities near Sanare, Estado Lara, 1500–1700 m; near Estánquez, Estado Mérida, 1500 m; and near Boconó [in the semi-isolated Macizo de Guaramacal, where several species of mammals show atypically high distributions, Soriano et al., 1990], Estado Trujillo, 2430 m; Anderson, 2003b). Notably, in the isolated Sierra de Aroa between the Cordillera de Mérida and the Cordillera de la Costa, records of *H. anomalus* reach only 800 m (Finca El Jaguar, 680–800 m; Anderson, 2003b). Future fieldwork at higher elevations in that range is likely to discover populations of some species of *Heteromys* in the mesic montane forests there (IGVSB, 2004), which have received very little sampling by mammalogists.

The ecogeographic patterns of *Heteromys catopterius* and *H. anomalus* described above beg for studies assessing the relative importance of climate, biotic interactions, and history in determining their distributions. Likely, all three classes of factors will prove important. Clearly, the localities that the species inhabit differ in climate. In addition, however, occurrence records intimate the possibility of competitive exclusion of *H. anomalus* from some areas of suitable habitat by *H. catopterius*. Finally, the absence of *H. catopterius* from some ranges likely derives from dispersal limitations. To distinguish between these hypotheses in particular regions, niche-based distributional modeling and considerations of sampling adequacy in a GIS framework are needed (e.g., Anderson et al., 2002a, 2002b; Anderson, 2003a; Graham et al., 2004; Phillips et al., 2006).

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NOTE ADDED IN PROOF: After this paper went to press, results of genetic studies by Duke S. Rogers and colleagues prompted us to reexamine specimens from the Guatopo region of the Serranía del Interior in Estado Miranda and Estado Guárico; based on these examinations, we reidentify two specimens as *Heteromys catopterius*, leading to modified biogeographic interpretations. TCWC 39720 (locality 78) and CM 78172 (locality 80) represent *H. catopterius*, but all other specimens from locality 80 correspond to *H. anomalus*. We confirm TTU and USNM specimens from localities 69 and 79 as *H. anomalus*, and our notes for the additional EBRG specimen from locality 69 as well as the MIZA specimen from locality 81 indicate that they match the diagnosis of *H. anomalus* as well. Many of these specimens constitute vouchers from important ecological, karyological, and genetic research, some of which should be reinterpreted based on these findings. Although the two vouchers for the copious ecological and natural history information provided by O'Connell (1981; see also Eisenberg et al., 1979) are both *H. anomalus* (locality 79), published phenetic and phylogenetic analyses based on allozymic data include specimens of both *H. catopterius* and *H. anomalus* from localities 78 and 80 (Rogers, 1990; Anderson et al., 2006; D. S. Rogers, in litt.). It remains unclear whether any of the standard karyotypes for Venezuelan *Heteromys* reported by Engstrom et al. (1987) derives from the lone specimen of *H. catopterius* from locality 80.

The discovery of *Heteromys catopterius* in this region holds several biogeographic implications. First of all, these specimens represent an extension of the known range of the species within the Serranía del Interior

ca. 70 km to the east. Here, *H. catopterius* is now documented from 400 m and 526 m on the northern slope of the Serranía del Interior (localities 78 and 80) and is sympatric with *H. anomalus* at the latter site (where habitat information for the two species is not available, unfortunately). In contrast, *H. anomalus* occurs at slightly higher elevations near the crest of the range on both the northern (710 m; 600–800 m; localities 79 and 81) and southern (680–720 m; locality 69) versants. Although with so few records it is not possible to characterize the species' distributions in the region in detail at present, they may coincide with local climatic differences and/or levels of habitat disturbance, as in other parts of their ranges. Notably, the northern faces of the coastal ranges, such as where *H. catopterius* has been collected at Guatopo, generally are wetter than the southern ones (Eisenberg et al., 1979; Huber, 1997; Ataroff-S., 2003; Meier, 2004). Presumably, *H. anomalus* also inhabits lower, slightly drier areas in the surrounding lowlands (e.g., locality 77, 50–70 m), but no nearby record of either species exists below 400 m.

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APPENDIX 1

Gazetteer and Specimens Examined in Principal Study Area

Here we report all specimens of *Heteromys* examined from central and eastern Venezuela (east of the Depresión de Yaracuy that separates the Cordillera de Mérida and Sierra de Aroa from the Cordillera de la Costa) and from Trinidad and Tobago (see Museum Specimens). Secondary information deriving from sources other than the collector is included in brackets and, where applicable, is followed by the source. Where original elevation was reported in feet, we provide that datum as well as the metric equivalent to the nearest whole number. Localities are numbered to correspond to figure 4, where they are plotted, and are arranged from north to south within states in Venezuela or major island in Trinidad and Tobago. For each entry, boldface type indicates the place name to which geographic coordinates correspond. We estimate that most coordinates are accurate to within 5 km (ca. 2 minutes); the placement of "ca." immediately before the coordinates indicates those accurate to an estimated 6–10 km. Museum catalog numbers for specimens examined follow each locality, using the abbreviations provided in Materials and Methods. Early specimens in the AMNH and USNM for which the osteological portion was cataloged in a separate numbering sequence from the skin are indicated as skin number/osteological number. See appendix 2 for specimens examined outside the principal study area.

Heteromys anomalus (total 993)
TRINIDAD AND TOBAGO (total 453)

Tobago

1. St. John Parish, **2.5 km SSW Charlottesville, Pigeon Peak**, Tobago Forest Reserve, 550 m, 11°18′N, 60°33′W, USNM 540705–540708; St. John Parish, **Charlottesville, 2.5 km SW [SSW], Pigeon Peak**, Tobago Forest Reserve, 550 m, 11°18′N, 60°33′W, USNM 540641–540643; St. John Parish, **Pigeon Peak**, 335–570 m [same coordinates; O. S., 1926; Goodwin and Greenhall, 1961; Voss, 1991], USNM 540721, 540722; and near Charllottesville [near **Pigeon Peak**; ca. 200–520 m; same coordinates; R.S. Voss field notes, 1989; Voss, 1991], AMNH 259985–259997.
2. **Spey Side** [= Speyside; ca. 0–300 ft (0–91 m); 11° 18′N, 60°32′W; O. S., 1926; Voss, 1991; not Goodwin and Greenhall, 1961], AMNH 184785.
3. **1.5 km S Pigeon's Peak** [ca. 800–1400 ft (244–427 m); 11°17′N, 60°33′W; O. S., 1926], USNM 538072.
4. St. Paul Parish, 4.5 km N Roxborough, **Roxborough Valley** and Ranch [< 1000 ft (305 m); 11°16′N, 60°35′W; displacement north of Roxborough likely road distance; coordinates correspond to midway point of Roxborough River at ca. 250 ft (76 m); O. S., 1926], USNM 540709, 540710.

Trinidad

5. **Caura** [600 ft (183 m); 10°43′N, 61°21′W; O. S., 1930; Goodwin and Greenhall, 1961; Voss, 1991], AMNH 7523, 7524, 7567/5960, 7568/5961, 7569/5962, 7570/5988, 7572/5964, 7573/5965, 7574/5966, 7575/5967, 7578/5970, 7579/5971, 7580/5972, 7581/5973, 7583/5975, 7584/5976, 7586, 7587/5978, 7588/5979, 7589/5980, 7590/5981, 7591/5982, 7592/5983, 7594/5985, 7596/5987, 7597, 7598/5989; BM(NH) 97.4.5.1 (= AMNH 7577/5969), 97.4.5.2 (= AMNH 7582/5974); MCZ B7775 (= AMNH 7593/5984), B7776; USNM 85570 (= AMNH 7585/5977); and St. George County, Tacarigua Ward, **Caura**, 600 ft [183 m; same coordinates], FMNH 5373, 5375.
6. N[orth] Ranges, **Guacharo Cave**, Aripo [= Aripo Cave; "about 3 miles (5 km) from the Aripo Valley Road"; Goodwin and Greenhall, 1961: 293; 2700 ft (823 m); 10°43′N, 61°15′W; coordinates correspond to indicated elevation on Cerro de Aripo, ca. 3 km NW of end of Aripo Road; Anonymous, unknown year; O. S., 1930; Goodwin and Greenhall, 1961], BM(NH) 33.12.4.8.
7. **Cumaca** [1200 ft (366 m); 10°42′N, 61°10′W; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 169704, 169717, 169727, 169738, 169739, 169768, 214451.
8. **St. Anne's Valley** [drained by St. Ann's River, which leads to populated area of same name on northeastern outskirts of Port-of-Spain; < 2000 ft (610 m); 10°41′N, 61°30′W; precise location in valley not available; coordinates correspond to midway point of St. Ann's River; O. S., 1930; Goodwin and Greenhall, 1961], USNM 21031/A36071.
9. Behind **St. Ann's** barracks; high road, close by **St. Anne's** barracks [suburb northeast of Port-of-Spain; ca. 200 ft (61 m); 10°40′N, 61°31′W; O. S., 1930; Goodwin and Greenhall, 1961], BM(NH) uncataloged "12.a" (holotype of *Mus anomalus*); and Botanic Gardens [= Royal Botanic Gardens; **North District, Port-of-Spain**; Goodwin and Greenhall, 1961; < 200 ft (61 m); same coordinates; O. S., 1930], BM(NH) 91.7.2.1, 92.9.7.10.
10. **Rio Grande**, near Tree Station [= Rio Grande Forest; 200 ft (61 m), 10°40′N, 61°05′W; O. S., 1930; Goodwin and Greenhall, 1961; not Voss, 1991], AMNH 174072; and **Rio Grande Forest**, Sangre Grande [same coordinates], AMNH 174073–174075.
11. **Matura** [150 ft (46 m); 10°40′N, 61°04′W; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 174070.
12. St. Pats [near **Arima**; 100 ft (30 m); 10°38′N, 61° 17′W; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 169675, 169678, 169687; and St.

Pats, **Arima** [same coordinates], AMNH 169674, 169682.

13. **Ravine Sable** Trace, Vega de Oropouche [50 ft (15 m) for Vega de Oropuche; 10°37′N, 61°04′W; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 186467.
14. Cornelliac Estate, **Vega de Oropouche** [50 ft (15 m); 10°36′N, 61°05′W; Anonymous, unknown year; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 188406; La Fortune Estate, **Vega de Oropouche** [same coordinates], AMNH 186468–186470; St. Andrew, **Oropuche [= Vega de Oropuche],** La Fortune Estate [same coordinates], UF 6571, 6572; and **Vega de Oropouche** [same coordinates], AMNH 186466.
15. **Cumuto** [100 ft (30 m); 10°35′N, 61°12′W; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 209004, 209005, 212306–212308.
16. **Sangre Grande** [100 ft (30 m); 10°35′N, 61°07′W; O. S., 1930; Goodwin and Greenhall, 1961; Voss, 1991], AMNH 174071; Maingot Estate, 5 miles [8 km] from **Sangre Grande** [ca. 10°35′N, 61°07′W; O. S., 1930; Voss, 1991], AMNH 174077–174088, 174091–174094, 174246–174248; and Maingot Estate, **Sangre Grande** [same coordinates], AMNH 174076, 174089, 174090, 186465.
17. **Fishing Pond** [< 100 ft (30 m); 10°35′N, 61°03′W; O. S., 1930], AMNH 174069.
18. St. George County, San Rafael Ward, **San Rafael**, 100 ft [30 m; 10°34′N, 61°16′W; O. S., 1930], FMNH 62050.
19. **North Manzanilla** [50 ft (15 m); 10°32′N, 61° 01′W; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 186446–186449.
20. **Manzanilla** [100–200 ft (30–61 m); 10°31′N, 61° 04′W; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 186471.
21. **Caparo** [150 ft (46 m); 10°27′N, 61°19′W; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 7522, 7562/5955, 7563/5956, 7564/5957, 7565/5958, 7566/5959, 22862.
22. **Bush Bush Forest**, Nariva Swamp [ca. sea level; 10°24′N, 61°03′W; O. S., 1930; Downs et al., 1968], AMNH 185471, 186626–186672, 186673 (skull 188377), 186674 (skull 188378), 186676 (skull 188379), 186677 (skull 186675), 186678–186713, 186714 (skull 188395), 186715, 186716 (skull 188396), 186717–186723, 186724 (skull 186726), 186725, 186727 (skull 188398), 186728 (skull 188399), 186729 (skull 188400), 186730 (skull 188402), 186731 (skull 188403), 188366, 188367, 188369–188376, 188380–188387, 188390–188394, 188397, 188401, 188404, 188405, 212136; **Bush Bush** [= Bush Bush Forest], Nariva Swamp [same coordinates], UF 6573; **Bush Bush** [= Bush Bush Forest; same coordinates], AMNH 203075–203079, 203081–203085, 203087–203101, 203103–203113, 204750, 204751, 204753–204763, 204765–204775, 204858–204879, 206598–206603, 206769–206775; and **Bush Bush Forest** [same coordinates], AMNH 186450–186464, 189318–189322, 235007–235009.
23. Victoria County, **Brickfield** [ca. 100–200 ft (30–61 m); 10°20′N, 61°16′W; O. S., 1930], FMNH 61899–61902.
24. **Mayaro** ["14 miles (23 km) east of Rio Claro on the Naparima–Mayaro Road at the 39-mile post"; Goodwin and Greenhall, 1961: 294; 50 ft (15 m); 10°18′N, 61°01′W; Anonymous, unknown year; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 235012–235014.
25. Princestown [= **Princes Town**; 100–150 ft (30–46 m); 10°16′N, 61°23′W; Anonymous, unknown year; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 1615–1619; Princestown [= **Princes Town**; same coordinates], AMNH 6003–6007, 6010–6017, 6021–6027; unmatched skull numbers AMNH 4730–4732, 4735–4742, 4746–4752; MCZ 27040 (= AMNH 7576/5968); USNM 85568 (= AMNH 6008/4733), 85569 (= AMNH 6019/4744); and St. George County, Savana Grande Ward, Princestown [= **Princes Town**; same coordinates], FMNH 5374, 5376.
26. **Cedros** [< 200 ft (61 m); O. S., 1930; precise location in Cedros Ward unavailable; approximate center of Ward has coordinates ca. 10°06′N, 61°48′W; Goodwin and Greenhall, 1961], AMNH 235010, 235011.
27. **Hollis Reserve** [not located; but note a Hollis Reservoir present at ca. 10°42′N, 61°11′W; Anonymous, unknown year], BM(NH) 95.22.
28. **Little Swamp, Cedros** [< 200 ft (61 m); O. S., 1930; not located; approximate center of Cedros Ward has coordinates ca. 10°06′N, 61°48′W; Goodwin and Greenhall, 1961], AMNH 235018.
29. **Lokano** [not located], BM(NH) 97.6.7.10.
30. **Turure Forest** [not located; but note Turure Ward, with approximate center at 10°32′N, 61°07′W; Goodwin and Greenhall, 1961], AMNH 235015–235017.
- . no specific locality, AMNH 204880, BM(NH) 37.11.11.5, 37.11.11.6, 37.11.11.7, 95.3.9.4.

VENEZUELA (total 540)

ANZOÁTEGUI

31. **Pekín** Abajo, Río Neverí, 100 m [10°09′N, 64° 31′W; DCN, 1972b], MHNLS 1395, 1421.
32. **Hato Capacho**, 2 km S [ca. 8 km ESE] de Urica [ca. 280 m; ca. 9°41′N, 63°56′W; DCN, 1968b], EBRG 21732.
33. Sabana de Río Caris, Hacienda **San Antonio** [ca. 160 m; 8°37′N, 64°04′W; DCN, 1966], MBUCV I-4740, 4741.
34. Río Caris, Paso **Los Cocos**, 280 m [ca. 120 m; DCN, 1966; 8°36′N, 64°04′W; S. Boher, in litt.; DCN, 1966; not Voss, 1991], MBUCV I-4745; Paso **Los Cocos**, Río Caris [same coordinates], MBUCV I-3121–3125; Paso **Los Cocos**, Río Caris, S El Tigre [same coordinates], MBUCV I-3496; and Río Caris, SE de Paso **Los Cocos** [same coordinates], MBUCV I-4744.
35. Río Caris, **Morichal Temblador** [tributary of the Río Hamaca, which is a tributary of the Río Pao, ca. 30 km W of the Río Caris; ca. 140–160

m; 8°34′N, 64°23′W; DCN, 1966], MBUCV I-4746.

36. Guayabal, **Hacienda San Antonio** [paso entre Guayabal y Los Tablones; S. Boher, in litt.], Río Pao, 100 m [8°31′N, 64°27′W; DCN, 1966; not Voss, 1991], MBUCV I-3126, 3127, 4742.
37. Río Caris, **La Ceiba** [not located; may be the site La Ceiba at ca. 80 m and 8°20′N, 63°59′W on Morichal La Ceiba, a tributary of the Río Limo, ca. 20 km W of the Río Caris; DCN, 1971d], MBUCV I-4747.
38. **Río Pao** [precise location along river not available], MBUCV I-4743.

Aragua

39. **Cumbre de Turiamo** [= Cerro La Cumbre; ca. 400 m; 10°26′N, 67°48′W; DCN, 1971b], EBRG 359, 360.
40. **3 km S Ocumare [de la Costa]**, sea level [10°26′N, 67°46′W; DCN, 1971b], USNM 517542.
41. Carretera Estación Biológica Rancho Grande–Cata, **La Trilla**, 50 m [10°24′N, 67°45′W; DCN, 1971b; Paynter, 1982], MIZA 20-273, 20-278; **La Trilla**, lado norte, Maracay, 50 m [same coordinates], MIZA 20-441; **La Trilla**, Parque Nacional Henri Pittier [same coordinates], MIZA 20-440; **La Trilla**, vía Ocumare [de la Costa]–Maracay, 50 m [same coordinates], MIZA 20-439; **La Trilla**, vía Ocumare [de la Costa]–Maracay, lado norte, 50 m [same coordinates], MIZA 20-437; and Vía Maracay–Cata, **La Trilla** [same coordinates], MIZA 20-274.
42. **Carretera Ocumare de la Costa, cerca a Ocumare**, 250 m [10°23′N, 67°45′W; coordinates correspond to indicated elevation near Ocumare de la Costa; DCN, 1971b], MIZA 20-223.
43. **Carretera Estación Biológica Rancho Grande–Cata, km 36**, Parque Nacional Henri Pittier, 300 m [10°23′N, 67°44′W; coordinates correspond to indicated elevation along road; DCN, 1971b], MIZA 20-277, 20-283; **Carretera Ocumare de la Costa**, Parque Nacional Henri Pittier, 250 m [same coordinates], MIZA 20-228; and **Km 36, vía Ocumare [de la Costa]–Maracay**, lado norte [same coordinates], MIZA 20-438.
44. **Carretera de Ocumare [de la Costa], ladera norte**, 630 m [10°22′N, 67°44′W; coordinates correspond to indicated elevation along road; DCN, 1971b], MIZA 20-342; and **Vía Ocumare de la Costa**, lado norte, 500 m [same coordinates], MIZA 20-224. See also locality 129 for specimens of *H. catopterius* from the same locality.
45. **Carretera de Ocumare [de la Costa], lado norte**, 920 m [10°22′N, 67°42′W; Beebe and Crane, 1947: 48; DCN, 1971b], MIZA 20-346; and **Carretera Estación Biológica Rancho Grande–Cata, km 24**, Parque Nacional Henri Pittier [900 m; see locality 130; same coordinates], MIZA 20-279. See also locality 130 for specimens of *H. catopterius* from the same locality.
46. **Vía Ocumare de la Costa** [N slope, R. Visbal, personal commun.], 695–750 m [10°21′N, 67°43′W; coordinates correspond to indicated elevation along road; DCN, 1971b], MIZA 20-227, 20-395.
47. **Estación Biológica Rancho Grande**, 13 km NW Maracay, 1050 m [10°21′N, 67°40′W; DCN, 1971b; Handley, 1976; but see Paynter, 1982], EBRG 15047–15049; and **Rancho Grande** [same coordinates], AMNH 144411. See also locality 137 for specimens of *H. catopterius* from the same locality.
48. Parque Nacional Henri Pittier, **4.6 km by road S Rancho Grande**, 750 m [10°20′N, 67°39′W; DCN, 1971b], EBRG 16955.
49. **Estación de Piscicultura** [= current Museo de la Estación Biológica Rancho Grande], El Limón [ca. 500 m; 10°19′N, 67°39′W; J. Sánchez-H., personal commun.; DCN, 1991], EBRG 131–133; **Estación Piscicultura** [= current Museo de la Estación Biológica Rancho Grande], El Limón, Maracay [same coordinates], EBRG 188; and Parque Nacional Henri Pittier, **Estación Piscicultura MAC** [Ministerio de Agricultura y Cría; = current Museo de la Estación Biológica Rancho Grande], El Limón [same coordinates], MIZA 20-004.
50. **El Limón**, 4 km NW Maracay, 524 m [10°18′N, 67°38′W; Paynter, 1982], USNM 517544.
51. **La Horqueta**, vía a Tiara, 1100 m [10°12′N, 67° 08′W; DCN, 1972a], MBUCV I-1554, 1555.
52. **Agua Amarilla**, carretera a Tiara [ca. 1080 m; 10° 11′N, 67°08′W; DCN, 1972a], MHNLS 454.
53. **Campamento Rafael Rangel** [Sierra Maestra; Brennan, 1952, 1957; = **Minas de Niquel**, R. Guerrero, in litt.], 1260 m [10°09′N, 67°09′W; DCN, 1972a; not Voss, 1992; or Adams and Lewis, 1995], USNM 317697–317699, 317701, 317703, 317705–317707, 317709, 317710; and **Campamento Rangel** [Sierra Maestra; Brennan, 1952, 1957; = **Minas de Niquel**, R. Guerrero, in litt.; same coordinates], USNM 314817. See also locality 138 for specimens of *H. catopterius* from the same locality.
54. **Carretera a Tiara** [precise location along road from La Victoria to Tiara not available; Tiara has coordinates of 10°08′N, 67°09′W; DCN, 1972a], MHNLS 1192–1194.

Carabobo

55. **Río Abajo**, 10 km [W] de Morón [< 40 m; 10° 29′N, 68°17′W; DCN, 1983], MBUCV I-4252; and **Río Abajo**, 10 km SW [W] de Morón [same coordinates], MBUCV I-4099.
56. **Agropecuaria Yapascua**, Ensenada Yapascua, E de Patanemo, 0 m [10°27′N, 67°54′W; J. Sánchez-H., personal commun.; DCN, 1971b], EBRG 8192; and **Agropecuaria Yapascua, Quebrada Yapascua**, al E de Patanemo, 50 m [same coordinates], EBRG 8171, 8193–8195.
57. Hacienda Saint Jean, **2 km SW de Borburata**, 40 m [10°26′N, 67°58′W; DCN, 1971b], EBRG 8167; and Hacienda Saint Jean, Borburata [= **2 km SW de Borburata**], 40 m [same coordinates], MHNLS 7351.

58. Bahía de **Patanemo**, 50 m [10°26′N, 67°55′W; DCN, 1971b], MHNLS 3737; and **Patanemo**, 10 m [same coordinates], MHNLS 3736, 3738, 3739.
59. **San Esteban**, northern Venezuela, 1500 ft [457 m; ca. 10°25′N, 68°01′W; coordinates correspond to indicated elevation SW (above) San Esteban; DCN, 1983; see also Phelps, 1944; Paynter, 1982], BM(NH) 11.5.25.149, 11.5.25.150; and **San Esteban**, northern Venezuela, hills, 1800 ft [549 m; same coordinates], BM(NH) 11.5.25.151.
60. **Las Quiguas** [650 ft (198 m); 10°24′N, 68°00′W; Allen, 1911; Paynter, 1982; DCN, 1971b; DCN, 1983], AMNH 31544, 31545.
61. Hacienda Saint Jean, **13 km [by road] SW de Borburata**, 120 m [10°24′N, 67°59′W; DCN, 1983; not Voss, 1991], EBRG 8186.
62. Fila la Josefina, **11 km [by road] NW Tronconero**, 1350 m [10°20′N, 67°55′W; J. Ochoa-G. and J. Sánchez-H., personal commun.; DCN, 1971b; DCN, 1991], MHNLS 7558, 7595; and Fila la Josefina, **11 km NW de Tronconero por carretera**, 1350 m [same coordinates], EBRG 10174, 10146, 10202.
63. La Florida, **Sierra Lorenzo de Bárbula**, 1050–1100 m [10°16′N, 68°03′W; coordinates correspond to indicated elevation SW of Bárbula, W of Naguanagua; DCN, 1975b; DCN, 1976a; DCN, 1976c; not Voss, 1992], MHNLS 2390, 2737.
64. Finca Cujigacho, **Guacara** [ca. 500 m; ca. 10°14′N, 67°52′W; DCN, 1991], MIZA 20-046.
65. 4.5 km SE Montalbán, **Sabana Aguirre**, 1055 m [correct elevation 562 m; A.L. Tuttle field notes, 1967; 10°11′N, 68°18′W; A.L. Tuttle field notes, 1967; DCN, 1976c; but see Handley, 1976], USNM 442100.

Cojedes

66. **Caño Hondo** [ca. 100–120 m; 9°32′N, 68°40′W; DCN, 1976b], TCWC 55661, 55662.
67. Hato El **Tirado** [ca. 100 m; 9°05′N, 68°25′W; DCN, 1963; not Voss, 1992], MHNLS 3892–3894.
68. **Hato Itabana** [38 km SE Las Vegas, Voss, 1991, 1992], 80 m [not located; unknown whether displacement from Las Vegas is airline or by road; not Voss, 1991, 1992, who gave coordinates for Las Vegas], MHNLS 4406.

Guárico

69. **50 km S and 39 km E Caracas**, near Guatopo National Park [= 15 km NW Alta Gracia, USNM archives; see also Handley, 1976], 680–720 m [10°01′N, 66°26′W; N.E. Peterson field notes, 1966; DCN, 1970b; see also Handley, 1976], EBRG 15075; USNM 387824–387827.
70. 23 km NE Calabozo, **Hato Los Leones**, Caño Agua Fría, 88 m [correct elevation 150 m; Handley, 1976; 9°03′N, 67°16′W; Handley, 1976], USNM 387822.
71. **Laguna Los Patos**, Estación Biológica los Llanos, Calabozo, 100 m [8°50′N, 67°22′W; DCN, 1970a; see also Handley, 1976], MBUCV I-1856.
72. **Hato Flores Moradas**, 50 km [by road] S Calabozo [ca. 60–75 m; 8°34′N, 67°33′W; DCN, 1971a; not Paynter, 1982], UF 23863.
73. **45 km [by road] S Calabozo** [= Fundo Pecuario Masaguaral; ca. 75 m; 8°34′N, 67°32′W; coordinates correspond to the two deciduous forest grids near Caño Caracol where *Heteromys* was captured; August, 1984; DCN, 1971a], TTU 33445.

Miranda

74. La Toma Capaya, **Río Marasmita**, 250 m [10° 28′N, 66°17′W; coordinates correspond to indicated elevation on Río Marasmita; DCN, 1970c], MHNLS 1791.
75. Valle de Sartenejas, **Universidad Simón Bolívar**, bosquecillo [ca. 1100 m; 10°25′N, 66°53′W; E. Pannier, personal commun.; DCN, 1964a; Aguilera et al., 1995b], MCNUSB I-414.
76. **8 km S Caracas, near Turgua** [= San Andrés, 16 km SSE Caracas; Handley, 1976], 1144 m [10°22′N, 66°50′W; Handley, 1976], USNM 387818.
77. **Estación Experimental Río Negro**, USR [Universidad Nacional Experimental Simón Rodríguez], 50–70 m [ca. 10°20′N, 66°17′W; DCN, 1970b; Ventura et al., 2002], MBUCV I-3633, 3634, 3636, 3637, 3639, 3641, 3684, 4021; **Estación Experimental Río Negro**, USR [Universidad Nacional Experimental Simón Rodríguez], a 30 km [by road] de Caucagua [same coordinates], MBUCV I-4129, 4130, 4188, 4206, 4251; **Estación Experimental Río Negro** [same coordinates], MBUCV I-3149; and **Estación Experimental Río Negro**, 20 km E Caucagua [same coordinates], MCNUSB I-822, 825, 1150.
78. **40 km [by road] N Altagracia** [de Orituco; near Agua Blanca; ca. 400 m; 10°04′N, 66°28′W; J.W. Sites, Jr. field notes, 1980; DCN, 1970b], TCWC 39720.
79. Parque Nacional Guatopo, **24 km N Altagracia** [710 m; 10°03′N, 66°26′W; coordinates correspond to the grid at the southern end of the park where *Heteromys* was captured; P.V. August, in litt.; O'Connell, 1981; not Paynter, 1982; or Musser et al., 1998], TTU 33446; and Parque Nacional Guatopo, by office [**24 km N Altagracia**; P.V. August, in litt.; same coordinates], TTU 35996.
80. **25 km [by road] N Altagracia de Orituco** [Parque Nacional Guatopo, near headquarters; ca. 526 m; 10°02′N, 66°27′W; J.W. Sites, Jr. field notes, 1980; DCN, 1970b], CM 78170–78173; TCWC 39719.
81. Parque Nacional Guatopo, **El Lucero** [ca. 600–800 m; 10°01′N, 66°27′W; DCN, 1970b], MIZA 20-037.

Monagas

82. **Cinco Cruces**, Distrito Caripe, 1100 m [10°16′N, 63°27′W; DCN, 1969b], MBUCV I-289.
83. **Cerro Espejo**, Distrito Caripe, 1550 m [10°11′N, 63°33′W; a Cerro Espejo exists along the Fila Macanillal ca. 15 km SE of Caripe but only reaches ca. 1200 m; coordinates given here correspond to indicated elevation along the Quebrada El Espejo, which drains the northen slope of a small mountain 3 km NW of Caripe and near other localities known for this collector (J. Ojasti); DCN, 1964c; DCN, 1964d], MBUCV I-291, 292.
84. **2 km N and 4 km W Caripe, La Laguna** [= 5 km NW Caripe; Handley, 1976], 1330 m [10°11′N, 63°32′W; N.E. Peterson field notes, 1967; DCN, 1964c; but see Handley, 1976], USNM 409819; and **2 km N and 4 km W Caripe**, near San Agustín [= 5 km NW Caripe; Handley, 1976], 1180–1260 m [same coordinates], USNM 409815, 409816. See also locality 159 for specimens of *H. catopterius* from the same locality.
85. **Campo Allegre** [= Campo Alegre; ca. 600 m; 10° 10′N, 63°43′W; a Campo Alegre exists in Estado Sucre ca. 10 km S of Cumaná (note locality 102); coordinates given here correspond to the Campo Alegre present in Estado Monagas (SE of the border with Estado Sucre) near San Antonio, as indicated in early reports of work by this collector (F.W. Urich); DCN, 1964c; Chapman, 1899; not Paynter, 1982], AMNH 14780.
86. **Cueva del Guácharo**, 1060 m [10°10′N, 63°33′W; DCN, 1964c; Aguilera et al., 1995b; not Handley, 1976], MBUCV I-281–287, 290; **Cueva del Guácharo**, Caripe, 1060 m [same coordinates], MBUCV I-288; **Cueva del Guácharo**, Caripe, 1065 m [same coordinates], MHNLS 1102–1104; **Cueva Guácharo** [same coordinates], MHNLS 807, 808; and 5 km W Caripe, **Cueva del Guácharo**, 1010 m [same coordinates], USNM 409820, 409821 (provisional identifications only for USNM 409820 and 409821; see Sympatry and Zones of Contact with *Heteromys anomalus*).
87. **Caripito** [ca. 20–80 m; 10°08′N, 63°06′W; DCN, 1969b; Paynter, 1982], AMNH 142630, 142631, 142633–142640; and **Caripito**, Wotr Camp [same coordinates], AMNH 142629.
88. Caripito [**road between Caripito and dock on Río San Juan**; J.W. Bickham field notes, 1980; < 20 m; 10°08′N, 63°04′W; DCN, 1969b], CM 78161–78163; TCWC 39712, 39713.
89. **San Antonio** [= San Antonio de Maturín], 1500–1800 ft [457–549 m; 10°07′N, 63°43′W; DCN, 1964c; Paynter, 1982], AMNH 69679–69693.
90. **Río Queregua**, Finca Doña Nar, 3 km W [SSW] El Tejero [ca. 200–280 m; ca. 9°37′N, 63°41′W; coordinates correspond to midpoint of the short Río Queregua, ca. 3 km SSW of El Tejero; DCN, 1968a], EBRG 22454, 22455.

Nueva Esparta

91. **2 km N and 2 km E La Asunción, Cerro Matasiete** [= 3 km NE La Asunción, Handley, 1976], 405 m [11°03′N, 63°51′W; DCN, 1979b; see also Handley, 1976], EBRG 15081; **2 km N and 2 km E La Asunción** [= **Cerro Matasiete**, 3 km NE La Asunción, Handley, 1976], 420 m [same coordinates], USNM 405982; and **3 km N and 2 km E La Asunción, Cerro Matasiete** [= 4 km NE La Asunción, Handley, 1976], 100 m [same coordinates], USNM 405981.
92. **Cerro Copey**, San Juan, 800 m [11°01′N, 63° 54′W; DCN, 1979b; but see Paynter, 1982], MHNLS 199.

Sucre

93. **Guarataro**, 8 km [by road] E San Juan de las Galdonas [ca. sea level; 10°43′N, 62°48′W; DCN, 1974a], MCNUSB I-1362.
94. **Playa Colorada, Guacuco**, Paria, 0–50 m [10° 42′N, 62°50′W; DCN, 1974a], MHNLS 6982, 6984, 6986–6989, 6994; and **Quebrada Colorada, Guacuco**, Paria, 50 m [same coordinates], MHNLS 6934.
95. **10 km N and 5 km E Güiria, near El Mango** [= 11 km NE Güiria, Handley, 1976], 35–45 m [10°40′N, 62°15′W; DCN, 1974b; not Handley, 1976], EBRG 15085; USNM 409810.
96. **Cristobal Colón** [= Macuro], 1500 ft [457 m; 10° 40′N, 61°58′W; coordinates correspond to indicated elevation above Macuro; DCN, 1974c; not Paynter, 1982], AMNH 36194–36196.
97. Distrito Valdez, población de **Macuro**, zona del balcón, vaquera, 50 m [10°40′N, 61°57′W; DCN, 1974c], MIZA 20-086; **Macuro**, Península de Paria [same coordinates], MIZA 20-055; and Población de **Macuro**, camino a la antena, el bebedero, 100 m [same coordinates], MIZA 20-087.
98. Entre Caricao y Chacopata [**carretera Cariaco–Chacopata, entre Chacopata y la Quebrada El Corral**, C. Ibáñez, in litt.; ca. sea level; ca. 10°39′N, 63°43′W; DCN, 1970d], MHNLS 6670.
99. **8 km N and 5 km E Güiria, Hacienda La Concordia** [= 9 km NE Güiria; Handley, 1976], 7 m [10°38′N, 62°15′W; Handley, 1976], USNM 409812; and **Ensenada Cauranta**, 9 km NE Güiria, 7 m [same coordinates], USNM 495294.
100. **26 km ESE Carúpano, Manacal**, 180–575 m [10° 37′N, 63°01′W; Handley, 1976], EBRG 16683–16690; **4 km S and 25 km E Carúpano, near Manacal** [= 26 km ESE Carúpano; Handley, 1976], 180–300 m [same coordinates], USNM 409849–409851; **5 km S and 24 km E Carúpano, Manacal** [= 26 km ESE Carúpano, Handley, 1976], 600 m [same coordinates], USNM 409839; **5 km S and 25 km E Carúpano** [= 26 km ESE Carúpano, Handley, 1976; same coordinates], EBRG 15092, 15098; **5 km S and 25 km E Carúpano, Manacal** [= 26 km ESE Carúpano, Handley, 1976], 180–600 m [same coordinates],

USNM 409826–409831, 409834, 409835, 409837, 409838, 409841–409843, 409845, 409846, 409848, 409852 , 409854; **5 km S and 25 km E Carúpano, near Manacal** [= 26 km ESE Carúpano, Handley, 1976], 185–600 m [same coordinates], EBRG 15089, 15091, 15093–15097; and **Manacal, 26 km ESE Carúpano**, 175–575 m [same coordinates], USNM 495296–495301, 495303, 495305, 495310, 495313–495319.

101. **Finca Vuelta Larga**, 9.7 km (by road) SE Guaraunos, 10 m [10°30′N, 63°07′W; DCN, 1969c; not Voss 1991, 1992], AMNH 257213–257218, 257222; MHNLS 8118, 8120, 8163, 8172; and **Finca Vuelta Larga**, 9.7 km [by road] SE Guaraúnos [same coordinates], MHNLS 8165, 8166, 8173, 8175.
102. Cumaná, **Campo Alegre**, 1350–1550 ft [411–472 m; 10°22′N, 64°12′W; a Campo Alegre exists at ca. 600 m in Estado Monagas near the border with Estado Sucre ca. 60 km SE of Caripe (note locality 85); coordinates given here correspond to indicated elevation at the Campo Alegre present ca. 10 km S of Cumaná near other localities known for this collector (E. André); DCN, 1964b; not Paynter, 1982], BM(NH) 0.5.1.42, 0.5.1.43, 0.5.1.44.
103. Cumaná, **Ipuré**, 2250 ft [686 m; ca. 10°22′N, 64°08′W; coordinates correspond to highest elevation (ca. 400 m) above town of Los Ipures; DCN, 1964b], BM(NH) 0.5.1.47, 0.5.1.48.
104. **40 km [by road] NW Caripito** [in hills near road marker km 81, ca. 36 km by road N of Río Caripe; J.W. Bickham field notes, 1980; ca. 40–200 m; 10°20′N, 63°20′W; DCN, 1969b, 1969c; ITMB, 2000; not Voss, 1992], CM 78164–78169; TCWC 39714–39718.
105. Cumaná, **Quebrada Secca** [= Quebrada Seca; = Villarroel; ca. 200 m; 10°18′N, 63°57′W; DCN, 1964c; see also Paynter, 1982], BM(NH) 0.5.1.49; **Quebrada Secca** [= Quebrada Seca; = Villarroel; same coordinates], AMNH 14759–14761, 14776–14779.
106. **Cumanacoa**, 700 ft [213 m; 10°15′N, 63°55′W; DCN, 1964c; Paynter, 1982], AMNH 69694–69696.
107. **Paujucillo**, Santa María de Cariaco [ca. 800 m; 10°15′N, 63°35′W; DCN, 1964c], MCNUSB I-768, 769.
108. **Cuchivano** ["at the foot of the slope on the southwest side of the valley a few miles from Cumanacoa" near Quebrada Juajua = Río Guasdua; Tate, 1931: 540], 700 ft [213 m; 10°14′N, 63°56′W; DCN, 1964c, unknown year b], AMNH 69647, 69648.
109. Los Palmales [near San Antonio, Santa Ana valley, **Los Dos Ríos**; 450 m; Wetmore, 1939; ca. 10°13′N, 63°52′W; DCN, 1964c; not Paynter, 1982; contra placement of Los Palmales in Estado Monagas by Phelps, 1944: 416–417], AMNH 14750–14758, 14762–14775.
110. Quebrada Yoraco, cerca de **Las Trincheras**, base Cerro Turimiquire [ca. 400 m; 10°12′N, 63°55′W; DCN, 1964c], EBRG 8196.
111. **Neverí**, 2400 ft [732 m; 10°11′N, 64°05′W; coordinates correspond to indicated elevation along Río Neverí; G.H.H. Tate field notes, 1925; DCN, 1969a; not Paynter, 1982; or Voss, 1988], AMNH 69649–69673.
112. **Cocollar** [= Cocoyar], 2600 ft [792 m; 10°11′N, 63°49′W; DCN, 1964c; see also Tate, 1931; not Paynter, 1982], AMNH 69674–69678.
113. **Latal** [= Quebrada Latal; = Quebrada Los Mangos; = Quebrada Panela], 3100 ft [945 m; 10°10′N, 63°57′W; G.H.H. Tate field notes, 1925; DCN, 1964c, unknown year a; not Paynter, 1982], AMNH 69697–69751.
114. **Mount Turumiquire** [= Cerro Turimiquire], 6000 ft [1829 m; 10°07′N, 63°53′W; DCN, 1964c], FMNH 38055.
115. Cumaná, **La Hormiga**, 2000 ft [610 m; not located], BM(NH) 0.5.1.45, 0.5.1.46.
116. **Serranía de Marigüitar**, 450 m [precise location within serranía not available; a locality at 450 m between town of Marigüitar and Cerro Marigüitar would have coordinates of ca. 10°22′N, 63°56′W; DCN, 1970d], MBUCV I-199, 200.

Vargas

117. **Camurí Grande**, Núcleo Universidad Simón Bolívar [ca. sea level; 10°37′N, 66°43′W; DCN, 1964a; Aguilera et al., 1995b], MCNUSB I-1011, 1110, 1148.
118. **Macuto** [ca. sea level; 10°36′N, 66°54′W; DCN, 1964a; not Paynter, 1982], USNM 102736.
119. **San Julián** [ca. 120 m; 10°36′N, 66°51′W; DCN, 1964a; but see Paynter, 1982], USNM 143793–143795.
120. **Canales de Naiguatá**, 720–750 m [ca. 10°35′N, 66°44′W; López-Fuster et al., 2000; see also DCN, 1964a; Valdez et al., 1985; not Voss, 1988], MHNLS 8539, 8569, 8574, 8582, 8587, 8590, 8593, 8596, 8599, 8600, 8602, 8603, 8610–8612, 8614, 8615, 8617, 8620, 8623, 8625–8629, 8631–8633, 8636, 8637, 8639, 8641, 8643–8645, 8648–8652, 8654, 8656, 8658, 8660, 8663, 8666–8668, 8673, 8675, 8677, 8679, 8681, 8685, 8686, 8688, 8690, 8694, 8695, 8698, 8699, 8702, 8705, 8706, 8708, 8709, 8715–8717, 8719, 8721, 8726; **Canales de Naiguatá**, vertiente N, Parque Nacional El Ávila, 720 m [same coordinates], MHNLS 8529–8531, 8534; **Los Canales de Naiguatá**, Parque Nacional El Ávila, 800 m [same coordinates], MBUCV I-2713, 2714, 2717; and Parque Nacional El Ávila, Sector Naiguatá [= **Los Canales de Naiguatá**], 720 m [same coordinates], MHNLS 4865, 4868, 4911, 4912, 4915. See also locality 160 for specimens of *H. catopterius* from the same locality.
121. **Carretera El Limón–Puerto La Cruz**, Hacienda El Limón, 300 m [10°32′N, 67°20′W; coordinates correspond to indicated elevation along road between El Limón and Puerto La Cruz; DCN, 1971c], MHNLS 1582; and **Suapo**, Hacienda El Limón, 100 m [same coordinates; coordinates correspond to indicated elevation on

Río Suapo; not Paynter, 1982], MHNLS 2482, 2587.

122. **Cagüita**, Hacienda El Limón, 300 m [10°31′N, 67°19′W; DCN, 1971c; but see Paynter, 1982], MHNLS 1841.
123. **3 km S and 46 km W Caracas**, near El Limón [= Hacienda Carapiche, 48 km W Caracas, Handley, 1976], 398 m [10°29′N, 67°19′W; Handley, 1976], USNM 387819–387821.
124. **La Cochinera**, Hacienda El Limón [small area with swine, W of Río El Limón, between El Limón and Las Llanadas; M. Lentino-R., in litt.], 500 m [10°28′N, 67°19′W; DCN, 1971c; Savini, 1999], MHNLS 2558; and **Las Llanadas**, Hacienda El Limón, 600 m [same coordinates; coordinates correspond to indicated elevation on Quebrada Las Llanadas; but see Paynter, 1982], MHNLS 2736, 2738, 2739.

Unknown state

—. No specific locality, BM(NH) 47.2.1.7 (skull 47.3.26.34; lectotype of *Perognathus bicolor*), 47.2.1.5 (lectoparatype of *Perognathus bicolor*), 47.2.1.4 (skull 47.3.26.35; lectotype of *Heteromys melanoleucus*), 47.2.1.6 (lectoparatype of *Heteromys melanoleucus*).

Heteromys catopterius (total 356)
VENEZUELA (total 356)

Aragua

125. Monumento Nacional **Pico Codazzi**, Colonia Tovar, 2425 m [10°25′N, 67°19′W; coordinates correspond to indicated elevation; DCN, 1971c], EBRG 22005.
126. Monumento Codazzi, ca. de la **Colonia Tovar**, 1800–2000 m [10°25′N, 67°17′W; DCN, 1971c], EBRG 21410–21422; Monumento Codazzi, **Colonia Tovar**, 1600–2000 m [same coordinates], EBRG 21736; and Monumento Codazzi, entrada **Colonia Tovar**, vía acueducto, 2000 m [same coordinates], EBRG 21408, 21409, 21423–21426, 21432–21434.
127. Monumento Nacional Pico Codazzi, **3 km SW Colonia Tovar** [1700–2100 m; 10°24′N, 67°20′W; DCN, 1971c; Moscarella-T. and Aguilera-M., 1999], MCNUSB I-1363, 1364.
128. Monumento Codazzi, **12.1 km vía Los Gabontes, Colonia Tovar**, 1730 m [10°23′N, 67°20′W; coordinates correspond to indicated elevation along road; DCN, 1971c], EBRG 21429, 21430.
129. **Carretera Estación Biológica Rancho Grande–Cata, km 29**, Parque Nacional Henri Pittier, 680 m [10°22′N, 67°44′W; coordinates correspond to indicated elevation along road; DCN, 1971b], MIZA 20-272, 20-276. See also locality 44 for specimens of *H. anomalus* from the same locality.
130. **Carretera de Ocumare [de la Costa], lado norte**, 920 m [10°22′N, 67°42′W; Beebe and Crane, 1947: 48; DCN, 1971b], MIZA 20-344; **Carretera Estación Biológica Rancho Grande–Cata, km 24**, 900 m [same coordinates], MIZA 20-270; **Carretera Estación Biológica Rancho Grande–Cata, km 24**, Parque Nacional Henri Pittier, 900 m [same coordinates], MIZA 20-275, 20-280, 20-281; **La Regresiva**, Rancho Grande [ca. 900–1000 m; same coordinates; R. Visbal, personal commun.; DCN, 1971b], EBRG 33; **Vía Ocumare de la Costa** [N slope, Schmid et al., 1992], 940 m [same coordinates; but see Schmid et al., 1992], MIZA 20-392, 20-393, 20-394; and **Vía Ocumare de la Costa**, vertiente norte, Parque Nacional Henri Pittier, 940 m [same coordinates; but see Schmid et al., 1992], MIZA 20-391. See also locality 45 for specimens of *H. anomalus* from the same locality.
131. Cerca del pluviometro de Andy Field, abajo de **Pico Guacamaya**, 1690 m [10°22′N, 67°40′W; DCN, 1971b; not Paynter, 1982], MIZA 20-375; Cerca del pluviometro de Andy Field, Parque Nacional Henri Pittier [near **Pico Guacamaya**], 1690 m [same coordinates], MIZA 20-373; Cerca del refugio, **Pico Guacamaya**, Parque Nacional Henri Pittier, 1730 m [same coordinates], MIZA 20-435; El refugio, **Pico Guacamaya**, Parque Nacional Henri Pittier, 1695 m [same coordinates], MIZA 20-376; **La Cumbre**, Estación Biológica Rancho Grande, 1500 m [same coordinates; R. Visbal, personal commun.], MIZA 20-436; Pico Limón [= **Pico Guacamaya**], Rancho Grande, [ca.] 13 km NW Maracay, 4900 ft [1494 m; same coordinates], USNM 517548–517552; and Vía **Pico Guacamaya**, Parque Nacional Henri Pittier, 1810 m [same coordinates], MIZA 20-374.
132. **Headwaters Río Limón**, [ca.] 13 km NW Maracay [ca. 1600 m; 10°22′N, 67°39′W; DCN, 1971b], USNM 517547.
133. Monumento Codazzi, **10 km vía Costa de Maya, Colonia Tovar**, 2110 m [10°22′N, 67°18′W; coordinates correspond to indicated elevation along road; DCN, 1971c], EBRG 21427, 21431.
134. Monumento Codazzi, **16.2 km vía Costa de Maya, Colonia Tovar**, 1840 m [10°22′N, 67°17′W; coordinates correspond to indicated elevation along road; DCN, 1971c], EBRG 21428.
135. **Palo Vaca** [straight stretch of road below La Regresiva, R. Visbal, personal commun.], Rancho Grande [ca. 800–900 m; 10°21′N, 67°42′W; DCN, 1971b], MBUCV I-1235.
136. **El Portachelo**, Rancho Grande, 14 km NW Maracay, 3708 ft [1130 m; 10°21′N, 67°41′W; C.O. Handley, Jr. field notes, 1960; DCN, 1971b; but see Paynter, 1982], USNM 517568; **El Portachuelo**, Parque Nacional Henri Pittier, 1100 m [same coordinates], MIZA 20-472; **El Portachuelo**, Rancho Grande, 14 km NW Maracay, 3708 ft [1130 m; same coordinates], EBRG 363; USNM 517553–517557, 517560–517562; Pico El Periquito, **El Portachuelo**, Rancho Grande [same coordinates], EBRG 191; Pico Periquito, **El Portachuelo**, Rancho Grande [same coordinates], EBRG 362; **Portachuelo**, Parque Nacional Henri Pittier, 1100–1120 m [same coordinates],

MCNUSB I-1326, 1327, 1329–1333; MIZA 20-217, 20-226, 20-234; Rancho Grande, **El Portachuelo** [same coordinates], MBUCV I-1249; and Rancho Grande, **Portachuelo**, 1100 m [same coordinates], MBUCV I-198.

137. **Rancho Grande**, 1080–1100 m [10°21′N, 67°40′W; DCN, 1971b; Handley, 1976; but see Paynter, 1982], AMNH 144848, 144853–144858, 144860, 144864–144868; EBRG 4317; KU 120294, 120295; MBUCV I-295, 1247, 2774, 2775; MCNUSB I-1056, 1057; UMMZ 110768–110773, 110781–110784; USNM 562956; UWZM S.31418; **Rancho Grande Biological Station**, 13 km NW Maracay, 1050 m [same coordinates], USNM 517543; **Rancho Grande**, near **Biological Station**, 13 km NW Maracay, 3576 ft [1090 m; same coordinates], USNM 517533–517535, 517536 (holotype of *Heteromys catopterius*) 517537–517541, 517545, 517546, 517558, 517559, 517563–517567, 517569; **Rancho Grande**, Parque Nacional Henri Pittier [same coordinates], MCNUSB I-1357; alrededores **Estación Biológica Rancho Grande** [same coordinates], EBRG 187, 190; Camino de La Cumbre, **Rancho Grande** [same coordinates], EBRG 189; **Estación Biológica Rancho Grande** [same coordinates], MCNUSB I-423, 424, 581; La toma, Parque Nacional Henri Pittier, **Estación Biológica Rancho Grande**, 1100 m [same coordinates], MIZA 20-173; La toma, **Rancho Grande**, Parque Nacional Henri Pittier, 1100 m [same coordinates], EBRG 10210; MIZA 20-130; Parque Nacional Henri Pittier, camino a la toma, **Rancho Grande**, 1100 m [same coordinates], MIZA 20-028; Parque Nacional Henri Pittier, **Estación Biológica Rancho Grande**, 1100 m [same coordinates], MIZA 20-024, 20-063; Parque Nacional Henri Pittier, **Estación Biológica Rancho Grande**, camino a la toma, 1100 m [same coordinates], MIZA 20-049; Parque Nacional Henri Pittier, más arriba de la **Estación Biológica [de Rancho Grande]**, 1300 m [same coordinates], MBUCV I-1795; Pico de Las Vegas, **Rancho Grande** [same coordinates], MBUCV I-1243–1246; Pico La Toma, **Rancho Grande** [same coordinates], EBRG 32; Toma de agua, **Rancho Grande**, Parque Nacional Henri Pittier, 1100 m [same coordinates], EBRG 4319; vicinity Maracay, **Rancho Grande** [same coordinates], UF 13709, 13710; and **Rancho Grande**, 13 km NW Maracay, 1080–1100 m [same coordinates], USNM 371016 (provisional identification only for USNM 371016; see Sympatry and Zones of Contact with *Heteromys anomalus*). See also locality 47 for specimens of *H. anomalus* from the same locality.

138. **Campamento Rafael Rangel** [Sierra Maestra, Brennan, 1952, 1957; = **Minas de Niquel**, R. Guerrero, in litt.], 1260 m [10°09′N, 67°09′W; DCN, 1972a; not Voss, 1992; or Adams and Lewis, 1995], USNM 317700, 317702, 317704, 317708, 317711, 317712; **Campamento Rangel** [Sierra Maestra; Brennan, 1952, 1957; = **Minas de Niquel**, R. Guerrero, in litt.; same coordinates], USNM 314815, 314816; and Loma de Hierro [= **Minas de Niquel**, J. Ochoa-G., in litt.], 10 km [by road] WNW [NNE] de Tiara, 1200 m [same coordinates], EBRG 16942. See also locality 53 for specimens of *H. anomalus* from the same locality.

139. **Carretera Choroní, hidrología** [precise location along road from Maracay to Choroní not available], MHNLS 4126.

140. **Parque Nacional Henri Pittier, carretera hacia Ocumare [de la Costa]**, 850 m [precise location along road not available; the indicated elevation on N slope near other known localities of *H. catopterius* would have coordinates of 10°21′N, 67°43′W; DCN, 1971b], MBUCV I-1791–1794.

Carabobo

141. **Campamento La Justa**, Rio Morón, 350 m [10° 23′N, 68°14′W; DCN, 1983; Bisbal-E., 1993], EBRG 17109, 17170, 17296.

142. **Parque Nacional San Esteban**, Cariaprima [1025 m; P.J. Soriano, in litt.; 10°22′N, 68°02′W; coordinates correspond to indicated elevation along Río Goaigoaza above Cariaprima; DCN, 1983], EBRG 22006.

143. **Campamento Palmichal**, Pica San Marcos, 780 m [10°20′N, 68°13′W; DCN, 1976c, 1983; Bisbal-E., 1993], EBRG 17189, 17297.

144. **Campamento Palmichal**, 1000 m [10°18′N, 68° 14′W; DCN, 1976c; Bisbal-E., 1993], EBRG 17135; and **Palmichal**, 23 km [by road] N Bejuma, 1000 m [same coordinates; not Musser et al., 1998], MIZA 20-064; USNM 562957.

Distrito Capital

145. **5 km S and 23 km W Caracas, Alto Ño León** [= 31 km WSW Caracas; 1870–1880 m; USNM archives; on S slope along Caracas–Tovar road, ca. 2.5 km W of junction with road to Caracaya; 10°26′N, 67°09′W; N.E. Peterson field notes, 1965, 1967; USNM archives; DCN, 1971c; but see Handley, 1976], EBRG 15082–15084.

Distrito Capital/Miranda

146. 1 km N Caracas, **Quebrada Chacaito**, 1170 m [10°32′N, 66°52′W; coordinates correspond to indicated elevation; DCN, 1964a; not Handley, 1976], USNM 405984, 405985; and **Quebrada Chacaito**, Parque Nacional El Ávila, 1200 m [same coordinates; coordinates correspond to indicated elevation], MHNLS 10064, 10068.

147. **Quebrada Chacaito**, 1050 m [10°31′N, 66°52′W; coordinates correspond to indicated elevation; DCN, 1964a; but see Handley, 1976], MHNLS 10599.

Distrito Capital/Miranda/Vargas

148. **Fila El Ávila, Parque Nacional El Ávila**, 1925 m [precise location in park along Fila El Ávila not available], EBRG 20892.

Distrito Capital/Vargas

149. **Boca de Tigre**, Fila El Ávila, Parque Nacional El Ávila, 1900 m [10°33′N, 66°54′W; DCN, 1964a, 1976a], MHNLS 10491–10493.
150. **El Junquito**, 1900 m [10°28′N, 67°05′W; Paynter, 1982; DCN, 1971c], MBUCV I-293.

Miranda (see also other localities shared with Distrito Capital)

151. **Hacienda Las Planadas** [= ca. 25 km (by road) N of Guatire; 1270 m; Rivas and Salcedo, 2006; 10°32′N, 66°30′W; coordinates correspond to indicated elevation; DCN, 1964a; DCN, 1979a], MCNUSB I-1570, 1571.
152. **19 km E Caracas, Curupao** [= 5 km NNW Guarenas, Handley, 1976], 1160–1260 m [10°31′N, 66°38′W; coordinates correspond to indicated elevation above Curupao; Handley, 1976; not Voss, 1991], EBRG 15079; USNM 387829–387831.
153. **Curupao** [ca. 500 m; 10°30′N, 66°38′W; DCN, 1964a; note that Curupao lies at the base of the Cordillera de la Costa in an area that is highly heterogeneous topographically and environmentally; precise collection locality (and corresponding elevation) not available], CUVC 11112.
154. **5 km S and 25 km W Caracas, Alto Ño León** [= 33 km WSW Caracas; 1958–1981 m; USNM archives; 10°26′N, 67°10′W; although other areas were sampled concurrently, these specimens derive from S slope, along Caracas–Tovar road, ca. 4.5 km W of junction with road to Caracaya; C.O. Handley, Jr., in litt.; N.E. Peterson field notes, 1967; USNM archives; DCN, 1971c; but see Handley, 1976], USNM 409802–409805, 409809; and **Alto Ño León, 33 km WSW Caracas** [1967 m, USNM archives; same coordinates], USNM 495293.
155. **Estación Experimental Jaime Hinao J.**, Facultad de Agronomía UCV [Universidad Central de Venezuela], El Laurel, carretera Hoya de la Puerta, 1355 m [10°23′N, 66°54′W; coordinates correspond to indicated elevation along road between Hoya de la Puerta and Cortada del Guayabo; DCN, 1995], EBRG 22259.

Miranda/Vargas

156. 9.4 km N Caracas, **Hotel Humboldt** [= 5 km NNE Caracas, Handley, 1976], 1982–2223 m [10°33′N, 66°52′W; although other areas were sampled concurrently, these specimens derive from an area NE of Hotel Humboldt, apparently near crest of El Ávila range possibly entirely within Estado Vargas, M.D. Tuttle field notes, 1965; DCN, 1964a; Handley, 1976], EBRG 15052–15056, 15059–15061, 15064, 15065, 15067–15070, 15073, 15074; USNM 370977, 370979–370981, 370983, 370984, 370987, 370988, 370990–370993, 370997–371000, 371003–371006, 371008, 371009, 371011–371013, 372492, 372494, 372495, 374689, 374690; 9.4 km [N] Caracas, **Hotel Humboldt** [= 5 km NNE Caracas, Handley, 1976], 2124 m [same coordinates], EBRG 15071, 15072; Pico Ávila, 5 km NNE Caracas, cerca **Hotel Humboldt**, 2124 m [same coordinates], EBRG 16681; Pico Ávila, 5 km NNE Caracas, near **Hotel Humboldt**, 2103–2221 m [same coordinates], USNM 495286–495288; and **Boquerón**, Parque Nacional El Ávila, 1970 m [same coordinates; DCN, 1964a, 1976a; see also SAGCN, 1994], MHNLS 10613.

Monagas

157. **San Agustín**, 5 km NW Caripe, 1270 m [10°12′N, 63°32′W; DCN, 1964c; Handley, 1976], USNM 495295.
158. **3 km N and 2 km W Caripe, Hacienda San Fernando** [= 3 km NW Caripe, Handley, 1976], 1320 m [10°12′N, 63°31′W; N.E. Peterson field notes, 1967; DCN, 1964c; but see Handley, 1976], USNM 409818.
159. **2 km N and 4 km W Caripe, La Laguna** [= 5 km NW Caripe, Handley, 1976], 1170–1335 m [10°11′N, 63°32′W; N.E. Peterson field notes, 1967; DCN, 1964c; but see Handley, 1976], EBRG 15088; USNM 409817, 409823; and **2 km N and 4 km W Caripe**, near San Agustín [= 5 km NW Caripe, Handley, 1976], 1170–1180 m [same coordinates], EBRG 15086, 15087. See also locality 84 for specimens of *H. anomalus* from the same locality.

Vargas (see also other localities shared with Distrito Capital and Miranda)

160. **Canales de Naiguatá**, vertiente N, Parque Nacional El Ávila, 720 m [ca. 10°35′N, 66°44′W; López-Fuster et al., 2000; see also DCN, 1964a; Valdez et al., 1985; not Voss, 1988], MHNLS 8532, 8533, 8535–8538; **Canales de Naiguatá**, 720 m [same coordinates], MHNLS 8576, 8583, 8585, 8586, 8588, 8589, 8591, 8592, 8595, 8597, 8601, 8605, 8606, 8616, 8618, 8621, 8622, 8624, 8634, 8638, 8642, 8647, 8653, 8655, 8657, 8661, 8662, 8669, 8670, 8672, 8676, 8678, 8680, 8683, 8684, 8687, 8689, 8691–8693, 8696, 8700, 8703, 8704, 8707, 8710–8714, 8720, 8722, 8725; **Canales de Naiguatá**, Parque Nacional El Ávila, 720–800 m [same coordinates], MBUCV I-2720–2724, 2726; MHNLS 8604, 8723; **Los Canales de Naiguatá**, 720 m [same coordinates], CUVC 11113; **Los Canales de Naiguatá**, Parque Nacional El Ávila, 800 m [same coordinates], MBUCV I-2715, 2716, 2718; Parque Nacional El Ávila, **Los Canales de Naiguatá**, 800 m [same coordinates], UV 11830 (= MBUCV I-2719), 11831 (= MBUCV I-2725); Parque Nacional El Ávila, Sector Naiguatá [= **Los Canales de Naiguatá**],

720 m [same coordinates], MHNLS 4866, 4867, 4913, 4914, 4916, 4917; Río Camurí Grande, **Los Canales de Naiguatá**, 15.6 km ramal este [same coordinates], MCNUSB I-1358; and **[Los Canales de] Naiguatá**, 720 m [same coordinates], MHNLS 4918. See also locality 120 for specimens of *H. anomalus* from the same locality.

161. **El Aguacatal**, Hacienda El Limón, 1400 m [10° 27′N, 67°16′W; DCN, 1971c], MHNLS 2684.
162. **Las Aguaitas**, Hacienda El Limón, 2000 m [10° 26′N, 67°18′W; coordinates correspond to indicated elevation on Río El Limoncito N of Colonia Tovar; DCN, 1971c; see also Paynter, 1982], MHNLS 2079, 3431; and **Las Aguaitas**, N Colonia Tovar, 2000 m [same coordinates], MHNLS 2441, 2614, 2615.

APPENDIX 2

Other Specimens Examined (Outside Principal Study Area)

See Gazetteer (appendix 1) for specimens examined from the principal study area.

Heteromys anomalus **(total 56): COLOMBIA (13):** Cundinamarca: Caparrapí, Volcanes, ICN 409, 1827–1831, 1832 (holotype of *Heteromys anomalus hershkovitzi*), 1833–1835, 1866; Magdalena: below Minca, 1000 feet [305 m], AMNH 15347 (holotype of *Heteromys jesupi*), 15348. **VENEZUELA (43):** Barinas: El Cobalongo, 7 km NNE Altamira [900 m, Handley, 1976; 8°53′N, 70°28′W; A.L. Tuttle field notes, 1967; DCN, 1975a; not Handley, 1976], USNM 416691; Falcón: El Mene [not located; multiple towns and geographic features named Mene are present in Estado Falcón], BM(NH) 26.12.6.1.; Lara: El Blanquito, 9 km [airline] SE de Sanare, Parque Nacional Yacambú, 1650 m, CVULA I-2728, 2732, 2736, 2742, 2743, 2750, 2754, 2755; El Blanquito, 17 km [by road] SE de Sanare, Parque Nacional Yacambú, 1600 m, CVULA I-6162; MCNUSB I-808, 809, 812, 813, 816, 852–855; El Blanquito, 17–18 km [SE by road] de Sanare, Parque Nacional Yacambú, 1500 m, EBRG 10302; Parque Nacional Yacambú [near El Blanquito; J. Ochoa-G., in litt.], 1500–1650 m, MBUCV I-4844, 4848, 4867; Trujillo: 10 km WNW Valera, Isnotú, 930 m, USNM 371034; Zulia: El Tucuco [= Los Ángeles del Tucuco], 46 km SSW Machiques, 300–400 m, CVULA I-1890; Misión Tukuko, 200–400 m, MHNLS 7711, 7781, 7803, 7806, 7808; USNM 448546, 448547, 448556, 448558, 448559, 448561; Río Aurare, FMNH 18622, 18623 (holotype of *Heteromys anomalus brachialis*), 18624–18627. See Anderson (2003b) for additional specimens from Colombia and western Venezuela.

Heteromys australis **(total 26): COLOMBIA (1):** Valle del Cauca: Las Lomitas, 5000 ft [1524 m], AMNH 32240 (holotype of *Heteromys lomitensis*). **ECUADOR (10):** Esmeraldas: San Javier [= San Javier de Cachaví], 60–120 ft [18–37 m], BM(NH) 1.3.19.19, 1.3.19.20, 1.3.19.21, 1.3.19.22, 1.3.19.23 (holotype of *Heteromys australis*), 1.3.19.24; USNM 113304–113307. **PANAMÁ (15):** Darién: Cana, 1800–2000 ft [549–610 m], USNM 178621, 178698, 178699 (holotype of *Heteromys australis consicus*), 178700, 179595; Amagal, 1000–2000 ft [305–610 m], ANSP 19491–19498, 19499 (holotype of *Heteromys australis pacificus*), 19779. See Anderson (1999) for additional specimens from Colombia, Panama, and western Venezuela; and Anderson and Jarrín-V. (2002) for additional specimens from Ecuador.

Heteromys desmarestianus **(species complex; total 87): COSTA RICA (11):** Cartago: Angostura, USNM 12903/38590, 12904/38591 (holotype of *Heteromys desmarestianus subaffinis*), 12905/36848; San José: Escazú, 3000 ft [914 m], AMNH 131729 (holotype of *Heteromys desmarestianus underwoodi*); Escazú, Los Higuerones, AMNH 137299–137302; San Gerónimo Pirris, USNM 250348 (holotype of *Heteromys desmarestianus planifrons*), 250349, 256445. **EL SALVADOR: (8):** Chalatenango: Los Esesmiles, 8000 ft [2439 m], MVZ 131116, 131117, 131119, 131121–131124, 131126 (paratypes of *Heteromys desmarestianus psakastus*). **GUATEMALA (1):** Alta Verapaz: Cobán, BM(NH) 43.6.13.1 (holotype of *Heteromys desmarestianus*). **MÉXICO (23):** Chiapas: Chicharras, USNM 77576 (holotype of *Heteromys goldmani*), 77577, 77579–77582, 77694; Mountains near Tonala, USNM 76062 (holotype of *Heteromys griseus*), 76063–76070; Oaxaca: Mountains near Santo Domingo, USNM 73381, 73382 (holotype of *Heteromys goldmani lepturus*); Tehuantepec, Mazatlán, AMNH 165995 (holotype of *Heteromys nigricaudatus*); Veracruz: Motzorongo, USNM 63718, 63719 (holotype of *Heteromys temporalis*), 63720; Unknown State: no specific locality, BM(NH) 56.8.1.13 (holotype of *Heteromys longicaudatus*). **NICARAGUA (1):** Matagalpa: Tuma, AMNH 28451 (holotype of *Heteromys fuscatus*). **PANAMÁ (43):** Colón: Río Indio, near Gatún, USNM 170919, 170920, 170975, 170976 (holotype of *Heteromys zonalis*); Chiriquí: Boquete, 4000–5800 ft [1219–1768 m], MCZ B10355, B10356 (holotype of *Heteromys repens*), B10358, B10360, B10361; Cerro Pando, ANSP 17835 (holotype of *Heteromys desmarestianus chiriquensis*), 17836, 17837, 18374–18377; Darién: Mount Pirri [= Cerro Pirre], near head of Río Limón, 4500–5200 ft [1372–1585 m], USNM 178998–179004, 179006–179015, 179016 (holotype of *Heteromys crassirostris*), 179018–179020; Panamá: Cerro Azul, 2500–3000 ft [762–914 m], USNM 171107 (holotype of *Heteromys panamensis*), 171108–171111, 171128. See Anderson (1999) for additional specimens from Colombia and Panama; and Anderson and Timm (2006) for additional specimens from Costa Rica.

Heteromys gaumeri **(total 7): MÉXICO (7):** Yucatán: Chichenitza [= Chichén Itzá], AMNH 12025/10458, 12027/10460, 12028/10461 (holotype of *Heteromys gaumeri*), 12029/10462, 12030/10463, 12031/10464; BM(NH) 97.4.5.3.

***Heteromys nelsoni* (total 2): MÉXICO (2): CHIAPAS**: Pinabete, USNM 77920 (holotype of *Heteromys nelsoni*), 77578.

***Heteromys nubicolens* (total 9): COSTA RICA (9): PUNTARENAS:** Monteverde, Monteverde Cloud Forest Reserve, Investigator's Trail, 1550 m. KU 159022–159024, 159025 (holotype of *Heteromys nubicolens*) 159026–159029; MNCR 1336; See Anderson and Timm (2006) for additional specimens from Costa Rica.

***Heteromys oasicus* (total 7): VENEZUELA (7): FALCÓN**: 49 km N, 32 km W of Coro, Cerro Santa Ana [= 15 km SSW Pueblo Nuevo], 550–615 m, EBRG 15110, 15111; USNM 456325 (holotype of *Heteromys oasicus*), 456327, 495338; Cerro Santa Ana, Península de Paraguaná, 420–550 m, EBRG 3705, 15984. See Anderson (2003b) for additional specimens from Venezuela.

***Heteromys oresterus* (total 10): COSTA RICA (10): SAN JOSÉ**: El Copey de Dota, 6000–6500 ft [1829–1981 m], UMMZ 64026, 64027 (holotype of *Heteromys oresterus*), 64028–64034, 66478. See Anderson and Timm (2006) for additional specimens from Costa Rica.

***Heteromys teleus* (total 17): ECUADOR (17): GUAYAS**: Cerro Manglar Alto, western slope, AMNH 64680–64693, 64694 (holotype of *Heteromys teleus*), 64695, 64696. See Anderson and Jarrín-V. (2002) for additional specimens from Ecuador.

APPENDIX 3

Descriptive Statistics for Primary Geographic Samples

Sample size, mean ± standard error, and range (minimum–maximum) for external variables, mass, cranial measurements, and one derived ratio for adult specimens in age class 4 from primary geographic samples of *Heteromys catopterius* (Rancho Grande and Humboldt) and *H. anomalus* (all other samples; see Materials and Methods and appendices 1 and 2 for provenience). Linear measurements are in millimeters, mass is in grams, and the ratio is multiplied by 100 to yield a percentage.

	Sample size	Mean ± standard error	Minimum–maximum
Total length			
Rancho Grande	25	302 ± 3	270–324
Humboldt	12	288 ± 2	275–300
Tukuko	10	280 ± 5	257–303
Yacambú	22	292 ± 3	262–323
Naiguatá	1	286 ± -	286
Neverí	10	292 ± 5	274–327
Latal	11	293 ± 3	279–312
Manacal	10	282 ± 5	258–302
Head-and-body length			
Rancho Grande	26	134 ± 2	113–149
Humboldt	12	126 ± 2	118–138
Tukuko	10	128 ± 2	118–140
Yacambú	22	131 ± 2	115–151
Naiguatá	1	134 ± -	134
Neverí	11	128 ± 3	117–147
Latal	11	130 ± 2	122–143
Manacal	10	126 ± 2	117–137
Tail length			
Rancho Grande	23	168 ± 3	147–192
Humboldt	12	163 ± 1	155–170
Tukuko	10	152 ± 3	136–172
Yacambú	22	162 ± 2	140–180
Naiguatá	1	152 ± -	152
Neverí	10	164 ± 2	155–180
Latal	11	163 ± 2	153–173
Manacal	10	156 ± 4	134–175
Tail length/head-and-body length, × 100 (%)			
Rancho Grande	23	126 ± 3	100–152
Humboldt	12	130 ± 2	112–141
Tukuko	10	119 ± 3	108–131
Yacambú	22	124 ± 2	109–140
Naiguatá	1	113 ± -	113
Neverí	10	127 ± 2	120–135
Latal	11	125 ± 2	113–137
Manacal	10	124 ± 3	108–146
Hind foot length			
Rancho Grande	26	36 ± 0	33–39
Humboldt	11	34 ± 0	32–36
Tukuko	10	35 ± 1	33–37
Yacambú	22	34 ± 0	32–37
Naiguatá	1	31 ± -	31
Neverí	11	35 ± 0	33–37
Latal	11	36 ± 0	34–37
Manacal	10	35 ± 1	33–38

APPENDIX 3
(Continued)

	Sample size	Mean ± standard error	Minimum–maximum
Ear length			
Rancho Grande	25	20 ± 0	16–22
Humboldt	12	17 ± 0	14–19
Tukuko	10	17 ± 0	15–18
Yacambú	21	19 ± 0	17–22
Naiguatá	0	–	–
Neverí	0	–	–
Latal	0	–	–
Manacal	10	19 ± 0	17–20
Mass			
Rancho Grande	19	82 ± 4	59–119
Humboldt	0	–	–
Tukuko	10	72 ± 4	58–100
Yacambú	20	57 ± 2	42–74
Naiguatá	0	–	–
Neverí	0	–	–
Latal	0	–	–
Manacal	10	60 ± 4	49–87
Occipitonasal length			
Rancho Grande	32	36.98 ± 0.15	35.13–38.66
Humboldt	14	35.87 ± 0.14	34.74–36.71
Tukuko	12	35.59 ± 0.50	31.94–39.02
Yacambú	22	34.65 ± 0.22	32.13–35.90
Naiguatá	17	34.84 ± 0.43	31.06–38.36
Neverí	11	36.35 ± 0.36	34.89–38.85
Latal	11	36.53 ± 0.25	35.15–37.90
Manacal	10	35.19 ± 0.46	32.85–38.04
Zygomatic breadth			
Rancho Grande	32	17.06 ± 0.09	16.07–18.17
Humboldt	14	16.05 ± 0.09	15.52–16.57
Tukuko	12	16.55 ± 0.23	15.12–17.90
Yacambú	22	16.20 ± 0.11	15.04–16.87
Naiguatá	17	15.76 ± 0.16	14.42–16.80
Neverí	11	16.68 ± 0.17	15.93–17.61
Latal	11	16.22 ± 0.15	15.46–16.89
Manacal	10	16.02 ± 0.18	14.90–16.95
Rostral length			
Rancho Grande	32	16.41 ± 0.09	15.26–17.57
Humboldt	14	16.01 ± 0.14	14.98–16.86
Tukuko	12	15.51 ± 0.23	13.94–17.01
Yacambú	22	15.41 ± 0.12	13.69–16.20
Naiguatá	17	15.41 ± 0.19	13.60–16.63
Neverí	11	16.29 ± 0.21	15.39–17.60
Latal	11	16.32 ± 0.16	15.38–16.97
Manacal	10	15.38 ± 0.24	14.48–17.00
Nasal length			
Rancho Grande	32	14.90 ± 0.09	13.70–15.93
Humboldt	14	14.21 ± 0.16	13.45–15.33
Tukuko	12	14.29 ± 0.24	12.74–16.10
Yacambú	22	14.10 ± 0.12	12.74–15.47

APPENDIX 3
(Continued)

	Sample size	Mean ± standard error	Minimum–maximum
Naiguatá	17	13.96 ± 0.22	11.93–15.35
Neverí	11	14.60 ± 0.22	13.79–16.04
Latal	11	14.81 ± 0.14	14.11–15.51
Manacal	10	14.00 ± 0.23	12.65–15.32
Least interorbital constriction			
Rancho Grande	32	9.29 ± 0.07	8.59–10.13
Humboldt	14	8.76 ± 0.07	8.13–9.05
Tukuko	12	8.68 ± 0.14	8.10–9.78
Yacambú	22	8.37 ± 0.05	7.99–8.78
Naiguatá	17	8.31 ± 0.08	7.81–8.87
Neverí	11	8.38 ± 0.11	7.89–9.00
Latal	11	8.53 ± 0.08	8.18–9.07
Manacal	10	8.00 ± 0.10	7.66–8.60
Squamosal breadth			
Rancho Grande	32	15.64 ± 0.07	15.02–16.56
Humboldt	14	15.09 ± 0.07	14.67–15.52
Tukuko	12	15.26 ± 0.14	14.13–16.00
Yacambú	22	14.85 ± 0.09	14.24–15.81
Naiguatá	17	15.02 ± 0.11	14.09–15.69
Neverí	11	15.08 ± 0.10	14.65–15.74
Latal	11	15.16 ± 0.09	14.46–15.50
Manacal	10	14.78 ± 0.13	14.21–15.45
Maxillary toothrow length			
Rancho Grande	32	5.60 ± 0.04	5.17–5.94
Humboldt	14	5.48 ± 0.05	5.14–5.70
Tukuko	12	5.42 ± 0.07	4.87–5.80
Yacambú	22	5.49 ± 0.05	5.04–6.05
Naiguatá	17	5.13 ± 0.05	4.67–5.45
Neverí	11	5.52 ± 0.06	5.26–5.83
Latal	11	5.47 ± 0.05	5.17–5.76
Manacal	10	5.21 ± 0.09	4.80–5.67
Interparietal width			
Rancho Grande	32	9.83 ± 0.09	8.57–11.01
Humboldt	14	8.49 ± 0.12	7.72–9.52
Tukuko	12	9.60 ± 0.13	8.85–10.30
Yacambú	22	8.59 ± 0.12	7.56–9.79
Naiguatá	17	8.67 ± 0.17	7.06–9.93
Neverí	11	8.71 ± 0.12	8.02–9.11
Latal	11	8.45 ± 0.10	7.94–8.97
Manacal	10	8.50 ± 0.14	7.70–9.33
Interparietal length			
Rancho Grande	32	5.04 ± 0.08	3.95–6.07
Humboldt	14	4.68 ± 0.09	3.95–5.17
Tukuko	12	5.22 ± 0.10	4.64–5.67
Yacambú	22	4.77 ± 0.08	4.03–5.51
Naiguatá	17	4.86 ± 0.11	4.09–5.63
Neverí	11	5.38 ± 0.06	5.13–5.83
Latal	11	5.11 ± 0.06	4.86–5.39
Manacal	10	5.27 ± 0.14	4.37–5.73

APPENDIX 3
(Continued)

	Sample size	Mean ± standard error	Minimum–maximum
Parietal breadth			
Rancho Grande	32	13.28 ± 0.07	12.61–14.00
Humboldt	14	12.68 ± 0.07	11.91–13.01
Tukuko	12	12.85 ± 0.15	12.29–13.94
Yacambú	22	12.53 ± 0.08	11.72–13.29
Naiguatá	17	12.34 ± 0.08	11.67–13.15
Neverí	11	12.61 ± 0.10	12.10–13.11
Latal	11	12.73 ± 0.10	11.97–13.05
Manacal	10	12.24 ± 0.06	11.97–12.47
Skull depth			
Rancho Grande	32	11.59 ± 0.04	11.09–12.07
Humboldt	14	11.03 ± 0.04	10.70–11.23
Tukuko	12	11.08 ± 0.10	10.35–11.65
Yacambú	22	10.99 ± 0.06	10.50–11.57
Naiguatá	17	11.01 ± 0.07	10.45–11.62
Neverí	11	11.16 ± 0.06	10.79–11.42
Latal	11	11.14 ± 0.08	10.52–11.48
Manacal	10	10.72 ± 0.10	10.36–11.40

APPENDIX 4

Descriptive Statistics for Los Canales de Naiguatá

Sample size, mean ± standard error, and range (minimum–maximum) of cranial measurements (in millimeters) for specimens in age classes 1–4 of *Heteromys anomalus* and *H. catopterius* from Los Canales de Naiguatá (localities 120 and 160; see appendix 1 for provenience).

	Sample size	Mean ± standard error	Minimum–maximum
H. anomalus, age class 1			
Occipitonasal length	9	28.33 ± 0.51	25.03–30.06
Zygomatic breadth	9	13.69 ± 0.19	12.54–14.41
Rostral length	9	11.73 ± 0.25	9.99–12.57
Nasal length	9	10.49 ± 0.25	8.87–11.42
Least interorbital constriction	9	7.35 ± 0.10	6.65–7.58
Squamosal breadth	9	13.33 ± 0.15	12.32–13.86
Maxillary toothrow length	9	4.72 ± 0.11	4.13–5.05
Interparietal width	9	8.24 ± 0.16	7.52–8.86
Interparietal length	9	4.58 ± 0.10	4.18–5.06
Parietal breadth	9	11.70 ± 0.09	11.02–11.92
Skull depth	9	9.97 ± 0.10	9.33–10.32
H. catopterius, age class 1			
Occipitonasal length	9	31.15 ± 0.32	29.32–32.59
Zygomatic breadth	9	14.87 ± 0.09	14.42–15.30
Rostral length	9	13.16 ± 0.13	12.43–13.59
Nasal length	9	11.41 ± 0.19	10.56–12.10
Least interorbital constriction	9	8.08 ± 0.09	7.68–8.45
Squamosal breadth	9	14.02 ± 0.08	13.61–14.38
Maxillary toothrow length	9	5.00 ± 0.10	4.40–5.34
Interparietal width	9	8.19 ± 0.08	7.79–8.42
Interparietal length	9	4.58 ± 0.10	4.28–5.07
Parietal breadth	9	12.50 ± 0.11	12.02–13.03
Skull depth	9	10.50 ± 0.10	9.88–10.85
H. anomalus, age class 2			
Occipitonasal length	13	30.48 ± 0.43	28.84–34.81
Zygomatic breadth	13	14.33 ± 0.14	13.68–15.45
Rostral length	13	12.97 ± 0.24	12.09–15.40
Nasal length	13	11.46 ± 0.23	10.57–13.59
Least interorbital constriction	13	7.61 ± 0.11	7.08–8.38
Squamosal breadth	13	13.85 ± 0.16	13.18–15.11
Maxillary toothrow length	13	5.00 ± 0.05	4.75–5.30
Interparietal width	13	8.44 ± 0.15	7.82–9.48
Interparietal length	13	4.63 ± 0.19	3.17–5.90
Parietal breadth	13	12.15 ± 0.12	11.23–13.05
Skull depth	13	10.30 ± 0.08	9.76–10.84
H. catopterius, age class 2			
Occipitonasal length	31	32.76 ± 0.27	30.40–36.29
Zygomatic breadth	31	15.35 ± 0.12	14.55–16.83
Rostral length	31	13.98 ± 0.14	12.48–15.68
Nasal length	31	12.19 ± 0.14	10.60–14.26
Least interorbital constriction	31	8.45 ± 0.07	7.76–9.47
Squamosal breadth	31	14.48 ± 0.09	13.82–15.87
Maxillary toothrow length	31	5.26 ± 0.03	4.83–5.57
Interparietal width	31	8.71 ± 0.10	7.30–9.45
Interparietal length	31	4.38 ± 0.09	3.12–5.26
Parietal breadth	31	12.86 ± 0.05	12.29–13.53
Skull depth	31	10.90 ± 0.06	10.16–11.64

APPENDIX 4
(Continued)

	Sample size	Mean ± standard error	Minimum–maximum
H. anomalus, age class 3			
Occipitonasal length	20	33.90 ± 0.43	31.07–37.21
Zygomatic breadth	20	15.16 ± 0.19	13.58–16.60
Rostral length	20	14.80 ± 0.22	12.75–16.66
Nasal length	20	13.49 ± 0.20	12.04–14.75
Least interorbital constriction	20	8.16 ± 0.10	7.35–9.09
Squamosal breadth	20	14.62 ± 0.12	13.70–15.84
Maxillary toothrow length	20	5.06 ± 0.07	4.51–5.60
Interparietal width	20	8.66 ± 0.10	7.57–9.41
Interparietal length	20	4.78 ± 0.08	4.14–5.52
Parietal breadth	20	12.25 ± 0.08	11.57–12.79
Skull depth	20	10.78 ± 0.07	10.22–11.51
H. catopterius, age class 3			
Occipitonasal length	5	35.22 ± 0.70	32.77–36.77
Zygomatic breadth	5	15.74 ± 0.21	15.05–16.22
Rostral length	5	15.36 ± 0.25	14.46–15.79
Nasal length	5	13.64 ± 0.52	12.44–15.52
Least interorbital constriction	5	8.82 ± 0.18	8.26–9.28
Squamosal breadth	5	15.02 ± 0.23	14.44–15.58
Maxillary toothrow length	5	5.31 ± 0.08	5.15–5.59
Interparietal width	5	8.87 ± 0.29	8.07–9.75
Interparietal length	5	4.77 ± 0.08	4.57–5.05
Parietal breadth	5	13.07 ± 0.16	12.61–13.49
Skull depth	5	11.29 ± 0.15	10.90–11.66
H. anomalus, age class 4			
Occipitonasal length	17	34.84 ± 0.43	31.06–38.36
Zygomatic breadth	17	15.76 ± 0.16	14.42–16.80
Rostral length	17	15.41 ± 0.19	13.60–16.63
Nasal length	17	13.96 ± 0.22	11.93–15.35
Least interorbital constriction	17	8.31 ± 0.08	7.81–8.87
Squamosal breadth	17	15.02 ± 0.11	14.09–15.69
Maxillary toothrow length	17	5.13 ± 0.05	4.67–5.45
Interparietal width	17	8.67 ± 0.17	7.06–9.93
Interparietal length	17	4.86 ± 0.11	4.09–5.63
Parietal breadth	17	12.34 ± 0.08	11.67–13.15
Skull depth	17	11.01 ± 0.07	10.45–11.62
H. catopterius, age class 4			
Occipitonasal length	5	37.77 ± 0.67	35.83–39.87
Zygomatic breadth	5	16.79 ± 0.18	16.25–17.37
Rostral length	5	16.76 ± 0.28	15.79–17.52
Nasal length	5	14.87 ± 0.32	13.94–15.58
Least interorbital constriction	5	9.00 ± 0.17	8.40–9.38
Squamosal breadth	5	15.23 ± 0.12	14.90–15.57
Maxillary toothrow length	5	5.43 ± 0.09	5.20–5.69
Interparietal width	5	9.21 ± 0.23	8.50–9.65
Interparietal length	5	4.80 ± 0.23	4.15–5.44
Parietal breadth	5	12.90 ± 0.15	12.60–13.37
Skull depth	5	11.65 ± 0.10	11.40–11.95

Chapter 3

Review of the *Oryzomys couesi* Complex (Rodentia: Cricetidae: Sigmodontinae) in Western Mexico

MICHAEL D. CARLETON[1] AND JOAQUIN ARROYO-CABRALES[2]

ABSTRACT

The status and distribution of eight species-group taxa of the *Oryzomys couesi* group (Rodentia: Cricetidae: Sigmodontinae) described from western Mexico are evaluated based on morphological and morphometric comparisons. Four of these are recognized as valid species within the region: *Oryzomys albiventer* Merriam, 1901 (including *molestus* Elliot, 1903), from inland plateau of the Mesa de Anáhuac; *O. couesi mexicanus* J.A. Allen, 1897 (including *bulleri* J.A. Allen, 1897; *lambi* Burt, 1934; *rufus* Merriam, 1901), from Pacific coastal plain, contiguous lower mountain slopes, and interior valleys along the Ríos Tepalcatepec–Balsas; *O. nelsoni* Merriam, 1898, from Isla María Madre; and *O. peninsulae* Thomas, 1897, from the southern tip of the Baja California Peninsula. Three other taxa named from uplands in interior Mexico—*aztecus* Merriam, 1901; *crinitus* Merriam; 1901; and *regillus* Goldman, 1915—are provisionally retained within *O. couesi*, but further study of their specific stature and relationships is required. The recommended taxonomic changes within western Mexico serve to discuss directions for future revisionary research that will refine the definition and distribution of *O. couesi* sensu stricto in Middle America.

INTRODUCTION

North and Middle American populations of the *Oryzomys palustris* group (sensu Merriam, 1901; Goldman, 1918) have been allocated to as many as 18 species (Merriam, 1901) or to as few as three (Hall, 1981). The systematic contributions of Goldman (1918) and Hall (1960) have played historically influential roles in reversing the early view of specific diversity within the *O. palustris* group. In his revision of the genus, Goldman (1918), perhaps emulating the revisionary model of *Peromyscus* as set forth by his colleague Osgood (1909), demoted many of Merriam's species to intergrading geographic races of the widely ranging, polytypic forms *O. couesi* and *O. palustris*. Within the *O. palustris* group, Goldman designated two sections, the *O. palustris* section, which contained the single North American species, and the *O. couesi* section, which contained the nominotypical species and six geographically isolated specific allies within Middle America (i.e., *O. antillarum*, *O. cozulmelae*, *O. fulgens*, *O. gatunensis*, *O. nelsoni*, and *O. peninsulae*). Goldman's specific classification was essentially maintained through the middle 1900s (Miller and Kellogg, 1955; Hall and Kelson, 1959). Subsequently, Hall (1960) considered *couesi* to be synonymous with *O. palustris* based on perceived intergradation of populations along coastal Texas in certain cranial and chromatic traits. Although argued within a very localized geographic context, Hall swept all of Goldman's (1918) subspecies of *couesi*, including those in western Mexico and Central America, under his expansive definition of *O. palustris*. His action set a broad-brushed precedent for assessing and taxonomically conveying morphological variation among populations of the *Oryzomys palustris* group. Soon

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afterward, other Middle American forms retained as species by Goldman (1918) or Hall and Kelson (1959) were pro forma brought into *O. palustris* as well (*cozumelae* by Jones and Lawlor 1965; *azuerensis* and *gatunensis* by Handley, 1966; *fulgens*, *nelsoni*, and *peninsulae* by Hershkovitz, 1971; *antillarum* by Hall, 1981).

Judged against today's standards of systematic documentation, presentation of data and analysis to support these sweeping taxonomic changes has been at best perfunctory, at worst nonexistent. Reexaminations of the purported zone of intergradation between *couesi* (*aquaticus*) and *O. palustris* (*texensis*) in Texas tellingly exposed the fragile underpinnings of such an inclusive definition of *O. palustris* (Benson and Gehlbach, 1979; Schmidt and Engstrom, 1994). As a result of these regional studies, *O. couesi* (Alston) was resurrected as a species distinct from North American *O. palustris* (Harlan), but most other Middle American taxa have remained as synonyms of a broadly ranging *O. couesi* (e.g., Honacki et al., 1982; Corbet and Hill, 1991; Musser and Carleton, 1993, 2005), an arrangement based on classificatory inertia rather than on actual documentation of consanguinity.

Herein, we review morphological and morphometric evidence for intergradation among forms of the *Oryzomys couesi* complex whose distribution lies in western Mexico. The region encloses striking topographic and biotic diversity and accordingly has proven to be strategic for unraveling specific diversity in other taxonomically problematic rodent genera, such as *Peromyscus* (Carleton, 1977; Carleton et al., 1982; Bradley et al., 1989, 1996) and *Sigmodon* (Zimmerman, 1970; Carleton et al., 1999; Peppers et al., 2002). Eight type specimens of species-group epithets currently allocated to Goldman's (1918) *O. couesi* section originate from this area (see fig. 1). In particular, we address the status and relationships of taxonomically recognized populations of *Oryzomys* that occur at the southernmost tip of Baja California (*O. couesi peninsulae*), on the Tres Marías Islands (*O. nelsoni*), along coastal lowlands in Sonora (*O. c. lambi*) and from Sinaloa through Oaxaca (*O. c. mexicanus*), and on the inland plateau region of Jalisco (*O. c. albiventer*). In addition, we discuss possible systematic affinities of other taxa named from uplands in interior Mexico—*O. c. regillus* (Michoacán), *O. c. aztecus* (Morelos), and *O. c. crinitus* (Distrito Federal).

Materials and Methods

Specimens that form the basis of this report principally consist of skins with their associated skulls and are contained in the following institutional and museum collections (abbreviation in parentheses): American Museum of Natural History, New York (AMNH); Carnegie Museum of Natural History, Pittsburgh (CM); Dickey Collection, University of California, Los Angeles (UCLA); Museum of Natural History, University of Kansas, Lawrence (KU); Field Museum of Natural History, Chicago (FMNH); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM, formerly the U.S. National Museum); the Natural History Museum, London (BMNH, formerly the British Museum of Natural History), and the University of Michigan Museum of Zoology, Ann Arbor (UMMZ). Type specimens and original series of most taxa described for populations of *Oryzomys* in western Mexico were examined firsthand, namely those of *albiventer* Merriam, 1901; *aztecus* Merriam, 1901; *bulleri* Allen, 1897; *crinitus* Merriam, 1901; *mexicanus* Allen, 1897; *nelsoni* Merriam, 1898; *peninsulae* Thomas, 1897; *regillus* Goldman, 1915; and *rufus* Merriam, 1901. Original topotypes of *lambi* Burt, 1934, were consulted, but we did not personally examine the holotype; William T. Stanley examined and measured the FMNH type of *molestus* Elliot, 1903, for us.

Approximately 600 specimens were examined (see registration numbers and full locality information under Taxonomic Summary) and measured, of which 284 adults were grouped into 11 geographically cohesive samples for univariate and multivariate analyses. According to current taxonomic understanding, these operational taxonomic units (OTUs), their abbreviations as employed in figures, specific localities, and sample sizes are recognized as follows:

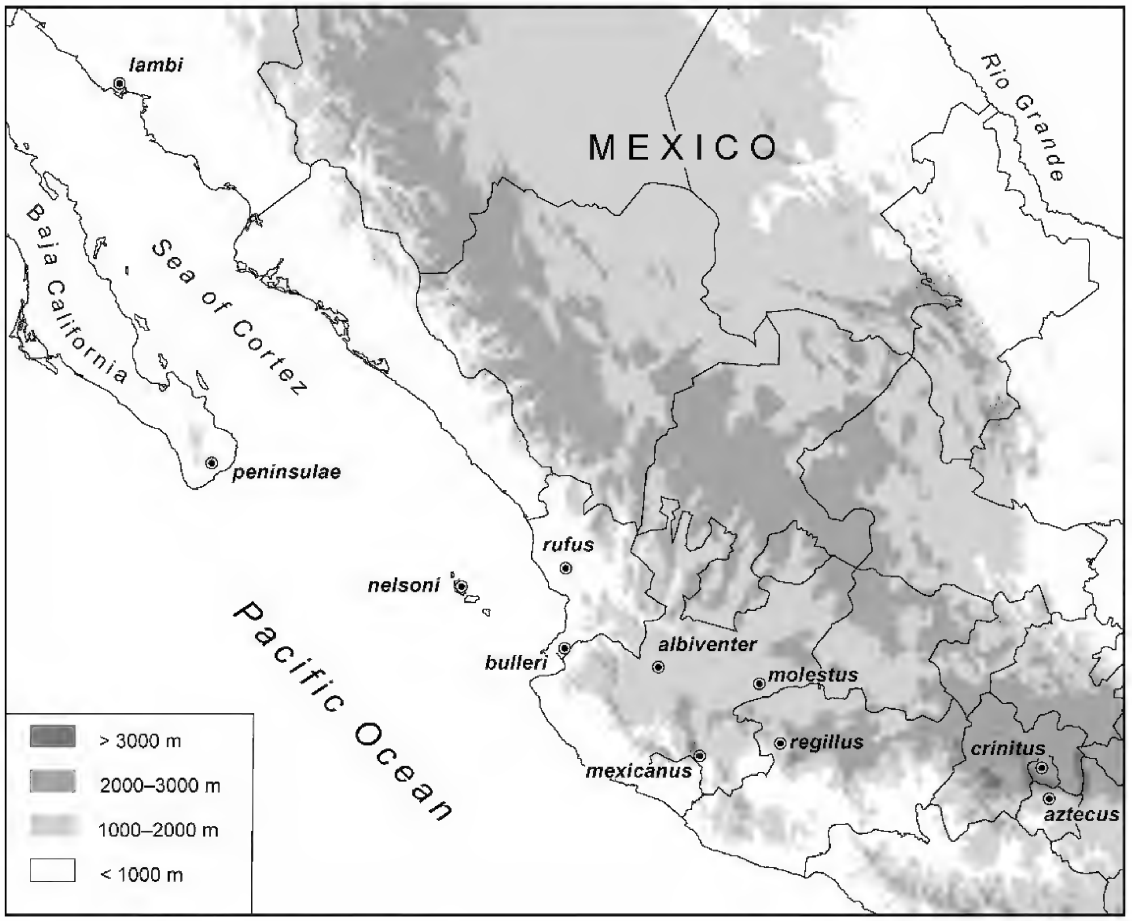

Fig. 1. Type localities of 11 taxa of the *Oryzomys couesi* species group described from western and central Mexico and discussed in the present study. Taxa and localities include: *albiventer* Merriam (1901) from Ameca, Jalisco; *aztecus* Merriam (1901) from Yautepec, Morelos; *bulleri* Allen (1897) from Valle de Banderas, Nayarit; *crinitus* Merriam (1901) from Tlalpan, Distrito Federal; *lambi* Burt (1934) from San José de Guaymas, Sonora; *mexicanus* Allen (1897) from Tonila, Jalisco; *molestus* Elliot (1903) from Ocotlán, Jalisco; *nelsoni* Merriam (1898) from Isla María Madre, Nayarit; *peninsulae* Thomas (1897) from Santa Anita, Baja California; *regillus* Goldman (1915) from Los Reyes, Michoacán; *rufus* Merriam (1901) from Santiago, Nayarit. Topography of Mexican sierras is indicated by 1000 m elevational bands.

Oryzomys couesi albiventer: (J3) Jalisco, Ameca, $N = 12$.

Oryzomys couesi mexicanus: (C1) Colima, vicinity of Santiago, $N = 33$; (C2) Colima, 5 mi NW Manzanillo, $N = 20$; (J1) Jalisco, localities to the N and E of Barra de Navidad, $N = 60$; (J2) Jalisco, Cuitzamala, $N = 20$; (N1) Nayarit, 1 mi S Cuautla, $N = 62$; (N2) Nayarit, San Blas and vicinity, $N = 23$; (N3) Nayarit, Chacala and Las Varas, $N = 16$; (N4) Nayarit, 2 mi E San Pedro Lagunillas, $N = 20$.

Oryzomys couesi peninsulae: (BC) Baja California Sur, San José del Cabo, $N = 14$.

Oryzomys nelsoni: (TM) Nayarit, Tres Marías Islands, Isla María Madre, $N = 4$.

Four external dimensions were transcribed from skin tags to the nearest whole millimeter (mm): total length (TOTL); tail length (TL); hindfoot length (HFL); and ear (pinna) length (EL). 17 cranial and three dental variables were measured to 0.01 mm (most are defined and illustrated in Carleton and Musser, 1995, and Musser et al., 1998), using

handheld digital calipers while viewing crania under a stereomicroscope. These measurements, and their abbreviations as used in text and tables, are: occipitonasal length (ONL); greatest zygomatic breadth (ZB); breadth of braincase (BBC); depth of braincase (DBC); breadth across occipital condyles (BOC); interorbital breadth (IOB); length of rostrum (LR); breadth of rostrum (BR); depth of rostrum (DR); length of incisive foramen (LIF); breadth across incisive foramina (BIF); length of diastema (LD); postpalatal length (PPL); length of bony palate (LBP); breadth of bony palate (BBP); breadth of zygomatic plate (BZP); length of auditory bulla (LAB); coronal length of maxillary tooth row (CLM); width of the upper first molar (WM1); depth of the upper incisor (DI).

Five age classes were defined according to stage of eruption of the upper third molar (M3) and relative wear of the upper molars (M1–3): (1) juvenile—M3 not erupted, or if erupted not reaching the occlusal plane; (2) immature—all molars fully erupted, little wear on M1–2 but no wear on M3; (3) young adult—upper molars, including M3, lightly worn, enamel pattern retaining well defined cusps and ridges, dentinal connections narrow; (4) full adult—M1–3 moderately to heavily worn with blunt cusps, wide dentinal connections, and enamel pattern variously obscured; (5) old adult—occlusal wear so advanced that the enamel pattern is largely obliterated, dentinal lakes of cusps are broadly continuous, and molars basinlike. We use the abbreviations M1–3 or m1–3 to individually reference the upper (maxillary) and lower (dentary) molars, respectively.

Standard descriptive statistics (mean, range, standard deviation) were derived for the 11 OTUs using only those specimens judged to be young, full, or old adult. External data are provided as general guidance to identification (table 1) but were not subjected to morphometric comparisons. Canonical variates (CVs) derived from multigroup discriminant-function classification and principal components (PCs) were computed using only the 20 craniodental variables, all of which were first transformed to natural logarithms. With only three specimens, the topotypes of *lambi* were entered as unknowns in the discriminant-function analysis and their probabilities of group membership calculated a posteriori, as were the holotypes of *aztecus*, *bulleri*, *crinitus*, *molestus* (as measured by W.T. Stanley, FMNH), *regillus*, and *rufus*. Principal components were extracted from the variance-covariance matrix, and variable loadings are expressed as Pearson product-moment correlation coefficients of the extracted components or canonical variates with the original cranial measurements. All analytical procedures were implemented using statistical routines contained in Systat for Windows, Version 10.2 (2002).

RESULTS AND COMPARISONS

Intrasample Age and Sex Variation: Superficial perusal of skulls in series of western Mexican *Oryzomys* reveals substantial range in size, shape, and pronouncement of cranial ridges, an impression remarked on by others who have worked with examples of *Oryzomys* (Merriam, 1901; Goldman, 1918; Paradiso, 1960; Park et al., 1974; Humphrey and Setzer, 1989). Some of this variation plausibly corresponds to the age of individuals, as suggested by occlusal wear of molars, but consistent size differences between the sexes are also evident and seemingly vary independently of age. Such casual visual impressions are reinforced by statistical comparisons among age and sex cohorts within our largest OTU of *O. couesi mexicanus* (N1, $N = 62$).

Many variables display regular, incremental increases in mean size across the three adult age classes defined, producing age-correlated differences that contribute substantially to nongeographic variation within our locality samples (table 1). The magnitude of F values and their significance levels differ according to major anatomical regions of the skull: most measurements taken on the facial region (LR, BR, DR, LIF, BIF, LD), which experiences substantial postweaning growth, disclose clear mean differences with greater age and achieve moderate significance levels, whereas those dimensions measured on the neurocranium (BBC, BOC, DBC, IOB), whose maturation plateaus earlier in postnatal development, exhibit slight or no increases

TABLE 1
Arithmetic Means of External and Craniodental Variables and Results of One-way ANOVAs for Sex and Age Cohorts in Adult *Oryzomys couesi mexicanus* from Nayarit
(OTU N1, $n = 62$; Y, A, and O = young, full, or old adult age class, respectively; see Materials and Methods for variable abbreviations.)

	Sex			Age			
Variable	M ($N = 31$)	F ($N = 31$)	f(sex)	Y ($N = 45$)	A ($N = 13$)	O ($N = 4$)	f(age)
TOTL	254.3	235.3	19.2***	241.7	248.5	268.5	4.1*
TL	129.9	120.3	15.1***	123.2	128.5	136.0	3.7*
HFL	31.0	30.0	15.5***	30.5	30.4	31.0	0.4
ONL	30.1	28.8	12.5**	29.2	29.8	31.8	6.9**
ZB	16.0	15.2	17.7***	15.5	15.7	16.5	2.9
BBC	12.6	12.4	4.4*	12.5	12.4	12.6	0.4
BOC	6.8	6.7	3.8	6.7	6.7	6.8	0.5
DBC	9.5	9.3	7.7**	9.4	9.4	9.6	0.6
IOB	4.8	4.6	18.4***	4.7	4.7	4.8	0.7
LR	9.5	8.9	11.8**	9.1	9.3	10.3	7.2**
BR	5.8	5.5	11.6**	5.6	5.7	6.2	4.6*
DR	6.6	6.3	9.6**	6.4	6.5	7.1	6.5**
LIF	6.0	5.7	10.2**	5.8	6.0	6.2	3.7*
BIF	2.3	2.3	1.9	2.2	2.3	2.5	7.3**
LD	7.9	7.3	18.5***	7.5	7.8	8.3	5.6**
PPL	10.0	9.5	11.6**	9.6	9.8	10.7	5.0**
LBP	5.5	5.1	16.7***	5.3	5.2	5.8	4.5*
BBP	5.5	5.4	3.8	5.5	5.5	5.6	1.5
BZP	3.3	3.1	5.9*	3.1	3.3	3.5	6.8**
LAB	4.1	4.0	1.1	4.0	3.9	4.2	3.8*
CLM	4.56	4.54	0.2	4.55	4.50	4.67	1.6
WM1	1.29	1.30	0.3	1.30	1.29	1.32	0.2
DI	1.85	1.79	3.8	1.77	1.89	1.99	8.7***

* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$.

with age and generally insignificant F values. Dimensions of the molars (CLM, WM1), which decrease in crown height with occlusal abrasion after eruption, do not grow in length and width, unlike osseous components of the skull; in contrast, the incisors substantially increase in girth with age (table 1). In nearly all of the age-sensitive variables, the significant differences reside between the young adult and full adult or old adult age classes, but not between the full adult and old adult age classes (according to Bonferroni post hoc multiple comparison tests). Such a pattern is predicated by sample sizes available for the three age groups and corresponding mean differences. We suspect that the underrepresentation of the old adult cohort in OTU N1 accounts for the fewer variables that exhibit significant age effects and the generally smaller F values. The imbalance among age classes and predominance of young adults in OTU N1 typify age representation across all our analytical samples (young adults comprise ca. 70%, full adults 25%, and old adults only 5% of all measured crania, respectively).

Moderate to strong differences between the sexes were derived for most cranial measurements of *Oryzomys couesi*, males averaging 4%–8% larger than females depending upon the variable used as an index of size (table 1). Interestingly, molar dimensions (CLM, WM1) are among those few variables that yielded no significant differences, a finding that indicates that females possess more robust dentitions relative to the head skeleton. Humphrey and Setzer (1989), on the other hand, did obtain significant differ-

ences for molar measurements, but their variable definition was an alveolar length that would reflect changes in the bony palate (ANOVAs of LBP were significant for age and sex effects; table 1). Our next largest sample of *O. couesi* disclosed the same pattern of sexual and age variation, variable differences according to anatomical region, and attained significance levels (J1, $N = 60$ or 58; results not tabulated). The larger size of male *Oryzomys* was qualitatively noted by early researchers (Merriam, 1901; Goldman, 1918; Paradiso, 1960) and quantitatively verified by Humphrey and Setzer (1989) in subspecies of *Oryzomys palustris*. Furthermore, growth studies of laboratory *Oryzomys palustris* have demonstrated that well-marked differences in weight and head-and-body length of males and females become apparent by approximately 3–4 weeks in age (Park and Nowosielski-Slepowron, 1972), or shortly after weaning when dispersing subadults are entering the trappable population. The occurrence of strong sexual dimorphism in *Oryzomys* contrasts with the pattern of nongeographic variation reported for other oryzomyines, in which conspicuous age-related size differences are demonstrable, but size disparity between the sexes is statistically trivial (e.g., *Microryzomys*—Carleton and Musser, 1989; *Oligoryzomys*—Myers and Carleton, 1981, Carleton and Musser, 1995; *Zygodontomys*—Voss, 1991). On average, there is a slight female bias (56%) among all adult skulls suitable for measurement, but the proportion varies appreciably among individual OTUs (33%–85% females).

Humphrey and Setzer (1989) procedurally circumvented the problematic variation introduced by consistent sexual size dimorphism in *O. palustris* by confining their analyses to adult males, an approach achievable with the large museum series available for a common North American species. Such selectivity proved impractical for several taxa of interest here and would severely limit their sample sizes for morphometric comparisons. Only four specimens of *nelsoni* and 21 of *peninsulae* will ever be available for study; the 26 examples of *albiventer* that we managed to assemble exemplify the relative rarity of this taxon in North American collections of Mexican *Oryzomys*. To explore possible biases in morphometric comparisons associated with imbalanced sex cohorts, we ran three iterations of discriminant-function analysis (using only females, only males, and both sexes) on three morphologically distinctive subspecies of *O. couesi* in western Mexico that vary in proportions of the sexes (*albiventer*, OTU J3 [4♀, 8♂]; *mexicanus*, OTUs C2 [17♀, 3♂], J2 [5♀, 15♂], N1 [31♀, 31♂]; *peninsulae*, OTU BC [10♀, 4♂]). Comparable and unambiguous phenetic structure among these five OTUs was disclosed in bivariate plots of the first two CVs extracted in each iteration (fig. 2), and the percent variation explained by the first two CVs is very similar in all three trials (81.1%–82.4%). Moreover, the hierarchy of craniodental phenetic resemblance among the five OTUs, based on Mahalanobis' distances between group centroids, is fully congruent. The exact clustering distances and relative disposition of OTUs on the first two CVs do differ according to the sexual subset analyzed, but such minor departures would be expected as a result of the different numbers of males and females available for each OTU and corresponding effects on covariance matrices.

In summary, we combined the sexes and three adult age classes in the following morphometric comparisons in order to amplify specimen numbers of the rarer taxa. Although the contributions of secondary sexual dimorphism and postweaning growth (age) to within-sample variation are statistically appreciable, those sources of variation are typically negligible relative to the extracted factors that emerged as taxonomically informative among samples. Indeed, the discriminant-function trials using one or the other or both sexes largely previewed the results we obtained with the full data set.

MORPHOMETRIC COMPARISONS: Pronounced disparity in size and pelage color was especially evident among populations in Jalisco, where key species-group taxa had been named (*albiventer* Merriam, 1901; *mexicanus* Allen, 1897), and initially sparked our suspicion about the possible existence of two species. Two well-defined morphologies were visually apparent in sorting locality samples: large-bodied, brightly colored specimens with broad skulls and robust molar rows versus

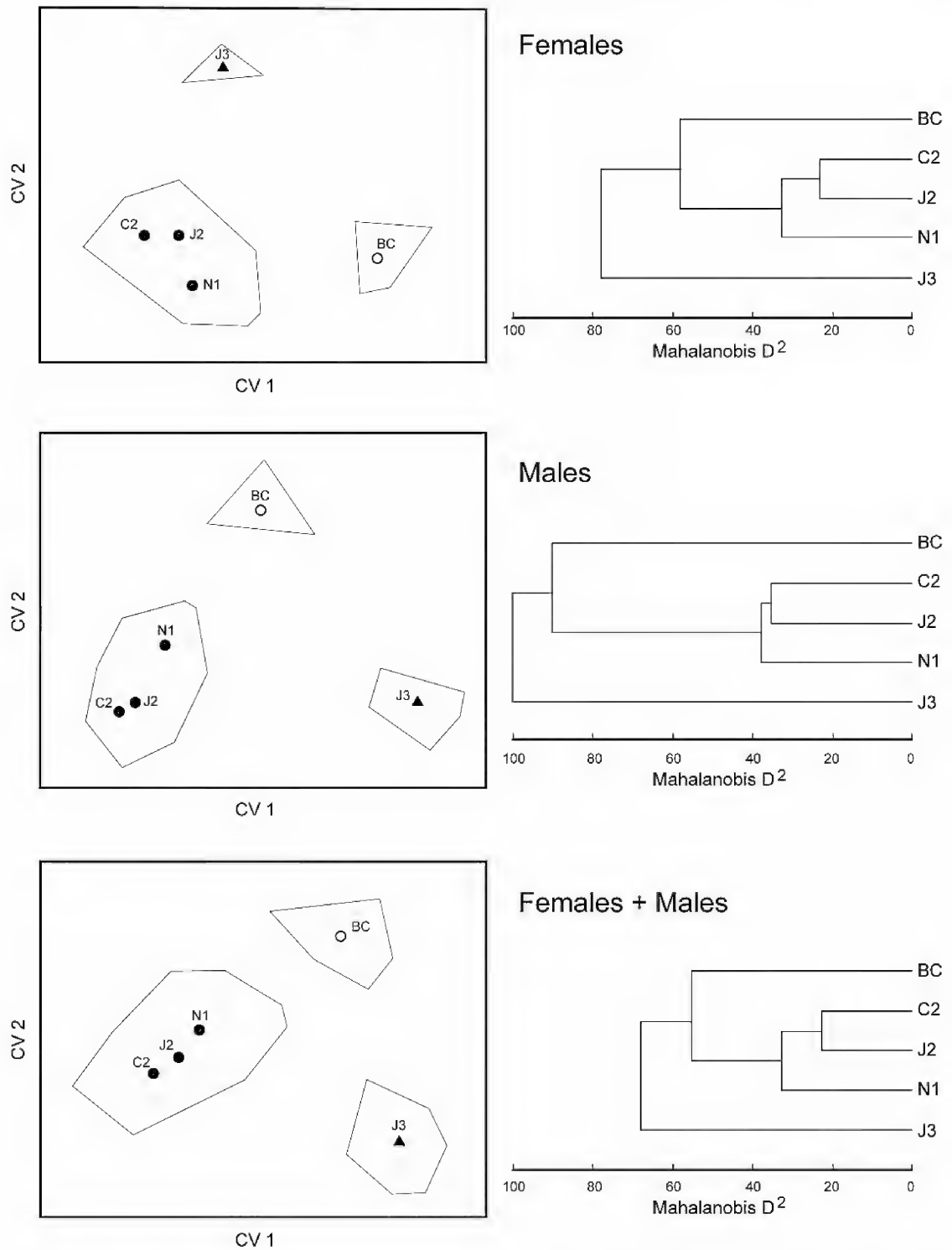

Fig. 2. Three iterations of discriminant-function analysis of select OTUs using only females, only males, and the sexes combined. Left column, projection of specimen scores onto the first two canonical variates extracted; right column, phenograms based on Mahalanobis distances among group centroids. See text for discussion.

smaller individuals with narrower skulls and more delicate molars (compare measurements for OTUs J1 and J3, table 2). Principal component ordination of all Jaliscan adults with intact skulls supplies additional evidence of substantial craniodental differentiation over small geographic distances. Projection of individual scores onto PCs I and II reveals two elliptical densities (fig. 3), one corresponding to specimens from the coastal plain and adjoining foothills in western Jalisco (= *mexicanus*, ca. sea level to 1000 m) and the other to those from uplands in central and eastern Jalisco (= *albiventer*, ca. 1200–1800 m). Although they marginally overlap, the major axes of these elliptical spreads are phenetically discrete (fig. 3), their Y-intercepts being significantly different between taxa (0.46 versus −1.68; $F = 25.2$, $P < 0.001$) while their slopes are comparable (0.65 versus 0.41; $F = 1.4$, $P = 0.245$). This covariation pattern among the specimens of *albiventer* and *mexicanus* is a familiar one that recalls multivariate contrasts recovered for other closely related, congeneric species of Muroidea (Voss et al., 1990; Voss and Marcus, 1992; Carleton and Musser, 1995; Carleton et al., 1999). Predictably, all variables load positively on the first component and most correlations are moderate to large ($r = 0.55$–0.98; table 3), indicating a general size factor. Although juveniles were omitted from our analyses, some postweaning growth still accounts for much of the elongate scatter observed within the species samples and for the oblique orientation of the group constellations on the first and second principal components. Those variables that load heavily on PC II, more or less orthogonal to the major axes of the taxon samples, emphasize the robust molars (CLM, WM1) of *albiventer* and, to a lesser extent, the relatively broader expanse of the incisive foramina (BIF) of *mexicanus* (tables 2, 3). The type specimen of *albiventer* (USNM 82236) nests comfortably among other large-bodied specimens from inland Jalisco (fig. 3). That of *mexicanus* (AMNH 2650/2128) was too damaged to include in the PCA, but its small molars (CLM = 4.63 mm, WM1 = 1.26 mm) conform to the smaller *Oryzomys* found commonly throughout the coastal lowlands of western Jalisco.

We expanded our geographic perspective by including other samples of the broadly ranging *mexicanus* and two forms with localized distributions in western Mexico, *nelsoni* from the Tres Marías Islands and *peninsulae* from the Baja Peninsula. The only analytically suitable locality series of *albiventer* remains Merriam's (1901) original type series (N = 12) from Ameca, Jalisco. Discriminant-function analysis of the 11 OTUs representing these taxa disclosed three well-defined clusters in the first three canonical variates extracted (fig. 4), which collectively summarize about 75% of the between-sample variation. The largest cluster consists of the eight samples that represent *mexicanus*. Their centroids are closely approximate and they broadly overlap one another in canonical scores; a posteriori misclassifications among the eight is commonplace (24%–92% incorrect depending upon the OTU). The *mexicanus* aggregation is entirely separate from OTU J3 of *albiventer* along the first canonical variate, a hiatus mainly reflecting the uniformly larger size of the latter (tables 2, 4), a distinction also emphasized in the first component derived from PCA of all Jaliscan specimens.

Although the sample of *peninsulae* is intermediate to those of *mexicanus* and *albiventer* in external size (table 2), cranial size and shape differences contribute to its sharp isolation from the latter OTUs along canonical variates 1–3 (fig. 4). Larger size in nearly all variables sets apart *peninsulae* from the various OTUs of *mexicanus* along the first canonical variate (correlations positive, coefficients moderately large; table 4). A subset of dimensions conveys certain shape differences that affect separation of *peninsulae* along the next two latent variates, including a deeper braincase (DBC), broader rostrum (BR), and expansive bony palate (LBP, BBP). Noteworthy are the absolutely and relatively broad incisive foramina (BIF) that characterize specimens of *peninsulae*, features that also contribute to the morphometric isolation of the Baja sample, especially on the second canonical variate (table 4). The incisive foramina in *peninsulae* even average wider than the large-bodied taxa *albiventris*

TABLE 2
External and Craniodental Measurements (in mm) of Samples of the *Oryzomys couesi* Complex in Western Mexico
(Sample statistics include the mean, ± 1 *SD*, and the observed range; variable abbreviations are defined in Materials and Methods; column headings reflect our taxonomic recommendations.)

	O. couesi mexicanus		*O. peninsulae*	*O. albiventer*	*O. nelsoni*
Variable	Jalisco (J1, $N = 58$)	Nayarit (N1, $N = 62$)	Baja California (BC, $N = 14$)	Jalisco (J3, $N = 12$)	María Madre (TM, $N = 4$)
TOTL	245.7 ± 25.1	244.8 ± 19.5	265.6 ± 22.3	285.4 ± 22.2	322 ± 28.8
	195–301	210–288	227–305	245–314	282–344
TL	132.3 ± 13.2	125.1 ± 10.7	136.8 ± 10.8	155.4 ± 14.3	181.5 ± 14.6
	102–160	105–150	114–156	129–173	160–191
HBL	113.3 ± 12.8	119.7 ± 11.0	128.9 ± 12.3	130.0 ± 8.2	140.5 ± 14.8
	91–141	96–144	113–152	116–142	122–153
HFL	30.2 ± 1.7	30.5 ± 1.2	32.0 ± 1.2	36.1 ± 1.9	37.3 ± 1.7
	26–34	27–33	29–34	33–40	35–39
ONL	29.4 ± 1.4	29.5 ± 1.5	31.5 ± 1.7	32.9 ± 1.3	34.8 ± 2.5
	26.4–32.5	26.7–33.2	27.8–34.3	30.0–34.5	31.7–37.8
ZB	15.8 ± 0.9	15.6 ± 0.8	17.1 ± 0.9	17.6 ± 0.6	18.0 ± 1.0
	13.8–18.0	13.9–17.9	15.1–18.7	16.6–18.3	16.6–18.9
BBC	12.5 ± 0.4	12.5 ± 0.4	12.9 ± 0.2	13.2 ± 0.3	13.4 ± 0.3
	11.7–13.5	11.7–13.3	12.4–13.3	12.8–13.8	13.0–13.6
BOC	6.7 ± 0.3	6.7 ± 0.2	6.8 ± 0.2	7.1 ± 0.2	7.2 ± 0.3
	6.1–7.3	6.3–7.2	6.2–7.0	6.9–7.6	6.8–7.6
DBC	9.1 ± 0.3	9.4 ± 0.4	9.9 ± 0.4	9.7 ± 0.3	10.0 ± 0.2
	8.3–9.8	8.4–10.5	9.4–10.8	9.3–10.1	9.9–10.2
IOB	4.7 ± 0.2	4.7 ± 0.2	4.9 ± 0.2	4.8 ± 0.2	5.2 ± 0.3
	4.1–5.1	4.3–5.3	4.7–5.3	4.5–5.1	4.8–5.6
LR	9.2 ± 0.6	9.3 ± 0.7	10.0 ± 0.7	10.3 ± 0.7	11.3 ± 0.9
	8.3–10.7	8.2–11.1	8.4–11.1	9.0–11.4	9.9–11.9
BR	5.8 ± 0.4	5.6 ± 0.4	6.4 ± 0.5	6.1 ± 0.3	7.0 ± 0.6
	5.0–6.7	4.8–6.9	5.4–7.4	5.4–6.5	6.2–7.5
DR	6.6 ± 0.4	6.5 ± 0.4	6.8 ± 0.5	7.1 ± 0.5	8.1 ± 0.7
	5.8–7.5	5.7–7.4	5 .7–7.7	6.2–7.7	7.0–8.7
LIF	5.8 ± 0.3	5.9 ± 0.4	6.4 ± 0.5	6.5 ± 0.4	6.4 ± 0.3
	5.0–6.5	5.0–6.7	5.5–7.3	5.7–6.9	6.1–6.9
BIF	2.2 ± 0.2	2.3 ± 0.1	2.6 ± 0.2	2.4 ± 0.2	2.5 ± 0.1
	1.9–2.7	2.0–2.7	2.3–3.2	1.9–2.6	2.4–2.6
LD	7.4 ± 0.5	7.6 ± 0.6	8.3 ± 0.7	8.3 ± 0.7	8.8 ± 0.7
	6.1–8.6	6.4–9.1	7.1–9.7	7.2–9.5	8.0–9.6
PPL	9.8 ± 0.7	9.7 ± 0.7	10.3 ± 1.0	11.0 ± 0.6	11.5 ± 1.0
	8.0–11.4	8.3–11.3	8.6–12.5	9.5–11.7	10.5–12.7
LBP	5.5 ± 0.3	5.3 ± 0.3	5.9 ± 0.3	6.2 ± 0.3	6.5 ± 0.6
	4.9–6.2	4.6–6.2	5.2–6.3	5.6–6.7	5.7–7.2
BBP	5.6 ± 0.2	5.5 ± 0.2	6.1 ± 0.2	6.0 ± 0.2	6.2 ± 0.2
	5.2–5.9	5.1–6.0	5.5–6.6	5.7–6.2	5.9–6.4
BZP	3.1 ± 0.2	3.2 ± 0.3	3.3 ± 0.3	3.7 ± 0.2	4.2 ± 0.3
	2.6–3.6	2.6–3.8	2.7–3.9	3.5–4.0	3.7–4.5
LAB	4.0 ± 0.1	4.0 ± 0.2	4.1 ± 0.2	4.5 ± 0.2	4.4 ± 0.3
	3.7–4.4	3.5–4.4	3.9–4.5	4.2–4.8	4.1–4.6
CLM	4.60 ± 0.14	4.56 ± 0.17	4.72 ± 0.11	5.24 ± 0.19	4.92 ± 0.12
	4.23–4.94	4.22–4.91	4.53–4.94	4.74–5.51	4.75–5.00
WM1	1.35 ± 0.05	1.30 ± 0.07	1.36 ± 0.05	1.53 ± 0.06	1.52 ± 0.04
	1.21–1.45	1.04–1.40	1.26–1.44	1.45–1.64	1.47–1.56
DI	1.75 ± 0.12	1.81 ± 0.14	2.18 ± 0.21	2.06 ± 0.13	2.31 ± 0.18
	1.53–1.98	1.54–2.19	1.83–2.59	1.83–2.26	2.06–2.47

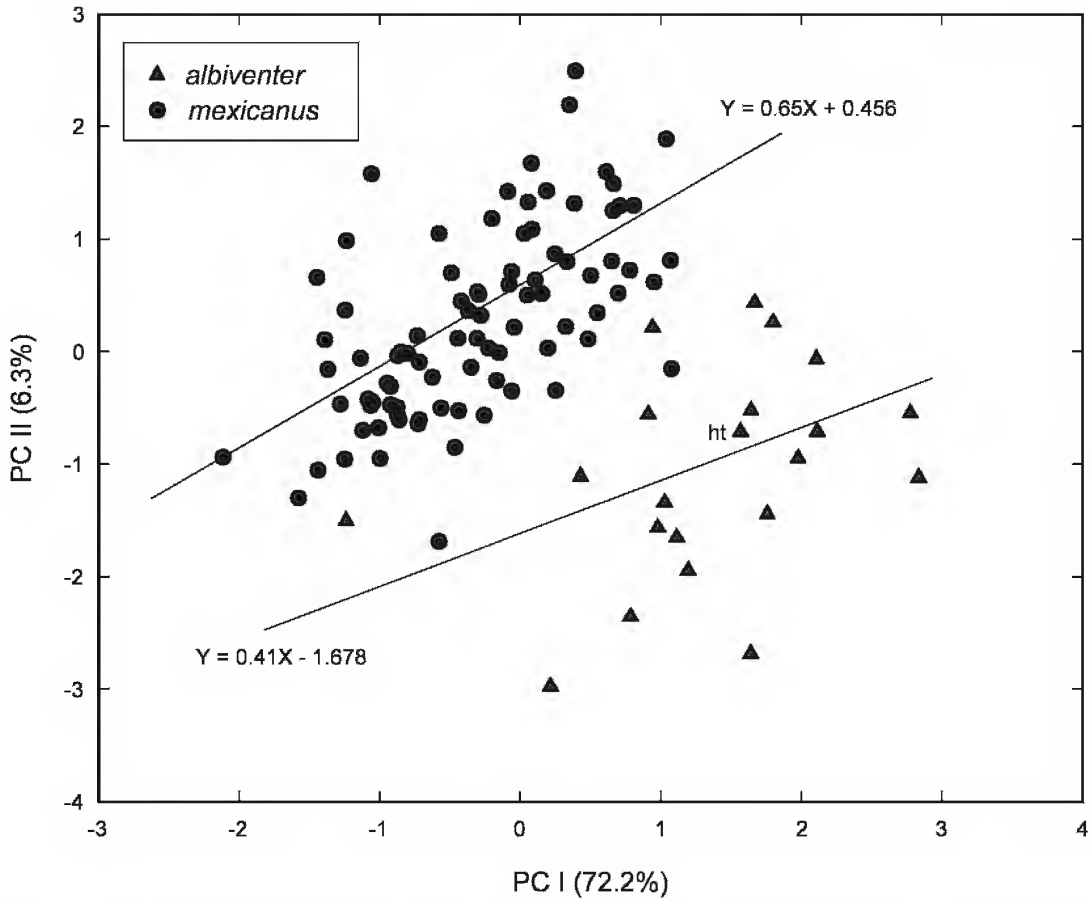

Fig. 3. Projection of specimen scores onto first two axes extracted from principal component (PC) ordination of 20 log-transformed variables as measured on intact skulls ($N = 108$) representing *Oryzomys couesi albiventer* and *O. c. mexicanus* from Jalisco, Mexico. The position of the type specimen (holotype) of *albiventer* Merriam (USNM 82236) is indicated by "ht." See table 3 for variable correlations and variance explained.

and *nelsoni* (table 2). Clustering (UPGMA) based on Mahalanobis' distances between centroids does indicate a closer phenetic affinity between *peninsulae* and OTUs of *mexicanus*, compared with *albiventris* and *nelsoni*, and simultaneously its strong differentiation from any one of them (fig. 5). In principal-component and discriminant-function analyses confined to samples of *peninsulae* and *mexicanus* (not illustrated), contrast in incisor girth (DI) emerges as an important variable for separation of the two taxa (table 4), in addition to those already mentioned. No specimen of *peninsulae* was mistakenly associated with another OTU according to post hoc probabilities of group membership.

Variable loadings that influence the isolation of *albiventris* similarly apply to the OTU of *nelsoni*, insofar as the first three variates extracted are concerned (fig. 4). Compared with examples of *mexicanus* and *peninsulae*, specimens of *nelsoni* and *albiventris* are large *Oryzomys* that possess more robust skulls and notably heavier molars (table 2), differences evidenced in the loadings on canonical variates one and two (table 4). Clear-cut circumscription of the four specimens of *nelsoni* from those of *albiventer*, however, is captured on the fourth and fifth variates (not plotted), which principally emphasize the massive development of the rostrum (LR, WR, DR, BZP) and upper incisors (DI) in *nelsoni* (tables 2, 4). Given the scope of taxa

TABLE 3
Correlations (Loadings) of 20 Log-transformed Craniodental Variables with Derived Principal Components (PC) Extracted from Ordination Using Intact Specimens ($N = 108$) of *Oryzomys couesi albiventer* and *O. c. mexicanus* in Jalisco, Mexico
(See fig. 3; variable abbreviations are defined in Materials and Methods.)

Variable	PC I	PC II
ONL	0.98***	0.03
ZB	0.94***	−0.02
BBC	0.75***	−0.09
BOC	0.71***	−0.05
DBC	0.84***	−0.03
IOB	0.59***	0.19
LR	0.93***	0.15
BR	0.87***	0.28
DR	0.92***	0.18
LIF	0.87***	0.12
BIF	0.65***	0.40**
LD	0.94***	0.15
PPL	0.93***	0.18
LBP	0.81***	−0.25
BBP	0.84***	−0.22
BZP	0.91***	−0.18
LAB	0.68***	−0.26
CLM	0.64***	−0.59***
WM1	0.55***	−0.65***
DI	0.87***	−0.11
Eigenvalues	0.069	0.006
% variance	72.2	6.3

*** $P \leq 0.001$; ** $P \leq 0.01$.

under consideration, covariation among these variables emerged as minor compared with the overarching patterns of between-group variation summarized by the first three canonical variates. Nonetheless, their unique and consistent expression in *nelsoni* accounts for its strong differentiation in the phenogram generated from Mahalanobis' distances between OTU centroids (fig. 5). The weak clustering association obtained between *nelsoni* and *albiventer* approximates that derived for *peninsulae* and OTUs of *mexicanus*.

Those type specimens with intact skulls were entered as unknowns in a 10-group discriminant-function analysis for classification according to a posteriori probabilities of group membership. The OTU of *O. nelsoni* was excluded as a classificatory option; furthermore, DI was omitted in calculating discriminant coefficients because the incisors in the type specimen of *aztecus* (USNM 51173) could not be measured. Type material of the three species-group taxa that originate within coastal plain were all definitely assigned to *mexicanus* (fig. 6), including the holotypes of *bulleri* Allen (AMNH 6663 to N3) and *rufus* Merriam (USNM 91404 to N2), as well as the three original topotypes of *O. couesi lambi* Burt (UCLA 51201 to N2, UCLA 51026 to C2, UCLA 51038 to J1); none demonstrated even a low level of affinity for the OTUs of *albiventer* or *peninsulae*. Those taxa described from upland localities in central Mexico were variously affiliated (fig. 6). The specimen of *molestus* Elliot (FMNH 8667), described from Ocotlán, Jalisco, was dispersed just peripheral to the type series of *albiventer* (Ameca, Jalisco) but definitely classified with that OTU ($P = 1.000$); the type of *albiventer* Merriam (USNM 82236) naturally clustered among the original type series. Type specimens of *aztecus* Merriam (USNM 51173, Yautepec, Morelos) and *regillus* Goldman (USNM 125945, Los Reyes, Michoacán) plotted at the margin of our large representation of *mexicanus*, but their canonical scores statistically aligned them with those OTUs (the greatest affinity of both with J2), not with *albiventer*. Finally, the holotype of *crinitus* Merriam (USNM 50182, Tlalpan, Distrito Federal) was associated with the series of *peninsulae*, at an unexpectedly strong level of probability ($P = 0.996$). The large values measured for the incisive foramen width (BIF), rostral breadth (BR), and braincase depth (DBC) of this specimen (table 5), variables that importantly contribute to the discrimination of *mexicanus* and *peninsulae* (see above), presumably influenced its multivariate disposition and a posteriori classification in *peninsulae*.

DISCUSSION

Taxonomic Recommendations and Future Study: We recognize four species among our study samples from western Mexico: *Oryzomys albiventer* Merriam, *O. couesi mexicanus* J.A. Allen, *O. nelsoni* Merriam, and *O. peninsulae* Thomas (figs. 7–9). These forms can be objectively defined by a combination of qualitative morphological traits, demonstrate cohesive patterns of morphometric identity,

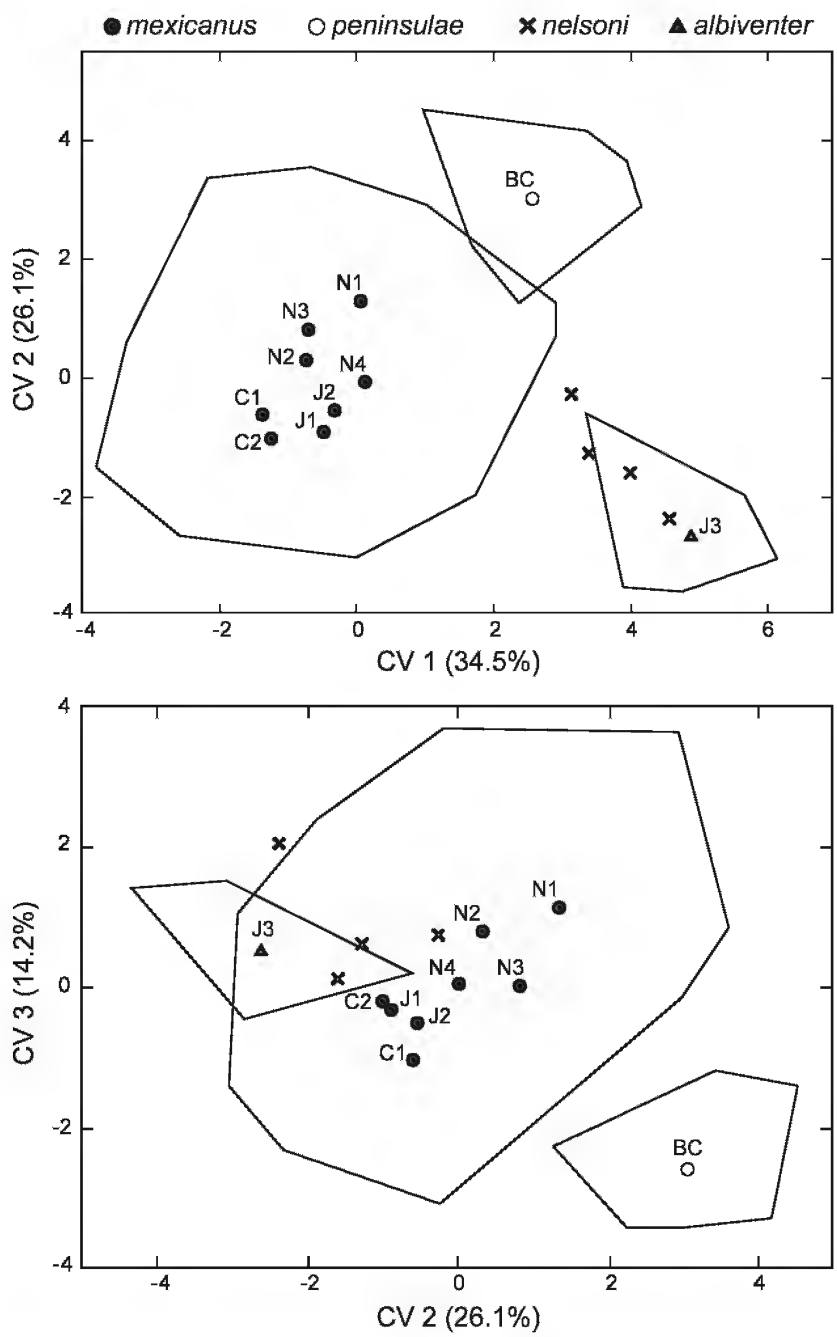

Fig. 4. Results of 11-group discriminant function analysis based on 20 log-transformed measurements of intact specimens (N = 246) representing the *Oryzomys couesi* group from western Mexico: *top,* projection of specimen scores on canonical variates (CV) 1 and 2; *bottom,* projection of specimen scores on canonical variates 2 and 3. Individual scores are plotted for the four known specimens of *O. nelsoni*; minimum convex polygons enclose individual scores around the centroid for OTUs of *albiventer* and *peninsulae*. To avoid visual clutter only centroids are indicated and a single bounding polygon encloses maximum dispersion for all specimens of *mexicanus*. See table 4 for variable correlations and variance explained.

TABLE 4
Correlations (Loadings) of 20 Log-tranformed Craniodental Variables with Derived Canonical Variates (CV)
(Based on 11-group discriminant function analysis of intact specimens, $N = 246$, representing *Oryzomys* in western Mexico; see fig. 4 for scatter plots of CVs 1–3. Variable abbreviations are defined in Materials and Methods.)

Variable	CV 1	CV 2	CV 3	CV 4	CV 5
ONL	0.69***	−0.07	−0.09	−0.22	0.27**
ZB	0.65***	−0.09	−0.22	−0.19	0.15
BBC	0.61***	−0.07	−0.05	0.09	0.25**
BOC	0.24*	−0.11	−0.01	0.13	0.20
DBC	0.65***	0.29***	0.04	0.05	0.13
IOB	0.46***	0.17	−0.03	−0.33***	0.27**
LR	0.59***	−0.11	−0.14	−0.16	0.28**
BR	0.46***	−0.05	−0.38***	−0.42***	0.29***
DR	0.55***	−0.16	−0.06	−0.33***	0.43***
LIF	0.62***	0.05	−0.15	−0.25**	0.01
BIF	0.56*	0.35***	−0.22*	−0.23*	0.16
LD	0.62***	0.05	−0.12	−0.23*	0.12
PPL	0.51***	−0.11	−0.04	−0.35***	0.15
LBP	0.65***	−0.29***	−0.31***	0.00	0.25**
BBP	0.70***	−0.05	−0.37***	−0.28**	0.16
BZP	0.62**	−0.08	0.12	−0.44***	0.13
LAB	0.62***	−0.21	0.03	−0.21	0.03
CLM	0.76***	−0.40***	−0.09	−0.11	−0.12
WM1	0.62***	−0.56***	−0.23*	−0.07	0.00
DI	0.75***	0.20	−0.15	−0.16	0.24**
Eigenvalues	2.19	1.66	0.91	0.73	0.41
Canonical Correlations	0.83	0.79	0.69	0.65	0.54
% variance	34.5	26.1	14.2	12.4	6.4

*** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$.

and occupy discrete geographic ranges (see emended diagnoses, distributions, and remarks under Taxonomic Summary). Such well-marked contrasts stand at odds with the conventional notion of intergrading subspecies as conveyed in past studies and influential classifications (Goldman, 1918; Hall, 1981). The genesis of the widely distributed, polytypic view of *O. palustris*, encompassing *couesi* and most other Middle American taxa, hinged on a geographically and taxonomically limited study (Hall, 1960) that was uncritically expanded in the latter 1900s (Handley, 1966; Hershkovitz, 1971; Hall, 1981), compelled more by the revisionary habit of the era than by fresh analyses of character data. Considered in this historical context, the sharp differentiation we encountered among western Mexican taxa, unexamined in any systematic detail since Goldman's (1918) revision, is unsurprising. These taxa have received minimal study since their descriptions; they are not "cryptic" species.

As now understood (i.e., Weksler et al., 2006, plus species recognized herein), *Oryzomys* is a moderately speciose genus (8 species to date considered valid). The distribution of most species is confined to Neotropical environments of Middle America, but one inhabits temperate settings in southeastern North America (*O. palustris*) and another occupies the northernmost margin of South America (*O. gorgasi*). Even so reconstituted, *Oryzomys* still contains several species-level uncertainties. The widely ranging, polytypic definition of *Oryzomys palustris*, as classically formulated in Hall (1981), reminds us of other Middle American species whose composite nature has been emphatically documented by recent researches. For example, *Oryzomys rostratus* has been separated from *O.* "*melanotis*" (Engstrom, 1984);

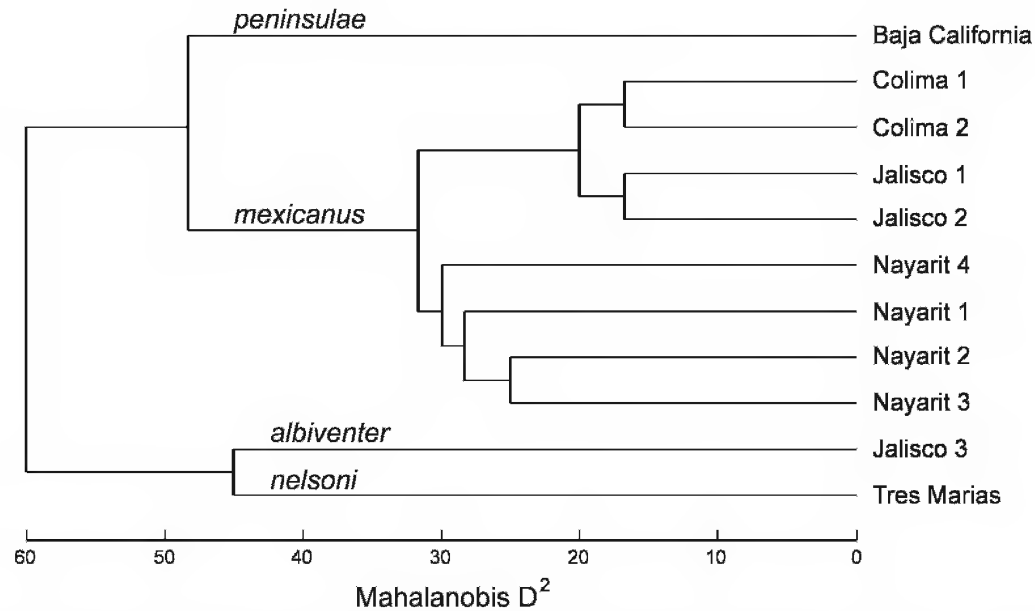

Fig. 5. Pattern of phenetic similarity among the 11 OTUs of *Oryzomys* from western Mexico based on UPGMA clustering of the squared Mahalanobis distances among group centroids as derived from discriminant-function analysis (see fig. 4). Currently recognized species-group taxa are shown above the appropriate stem subtending terminal OTUs.

Sigmodon arizonae, *S. hirsutus*, *S. mascotensis*, and *S. toltecus* have been recovered from *S.* "*hispidus*" (Zimmerman, 1970; Carleton et al., 1999; Peppers and Bradley, 2000; Peppers et al., 2002; Carroll et al., 2005); and *Peromyscus aztecus*, *P. beatae*, *P. levipes*, *P. madrensis*, *P. sagax*, *P. simulus*, and *P. spicilegus* have been resurrected as valid species, all of them formerly masked under *P.* "*boylii*" (Carleton, 1977, 1979; Carleton et al., 1982; Rennert and Kilpatrick, 1987; Schmidly et al., 1988; Bradley et al., 1989, 1996; Castro-Campillo et al., 1999). In similar fashion, future taxonomic research upon *Oryzomys*, in particular the *O. couesi* section, will undoubtedly disclose greater systematic diversity, and some of those research avenues might explore or solidify the following points:

(1) The remoteness of the *Oryzomys* population that once existed at the tip of Baja California, far removed from the core generic distribution in mainland Mexico, prompted Nelson (1922: 124) to remark that it "may readily have been introduced in shipments of bananas or other farm products from Mazatlan or elsewhere along the mainland coast, where a related species [i.e., *O. couesi mexicanus*] is plentiful." His conjecture on the nonnative status of the peninsular form may have influenced Hall (1981) to arrange it within a polytypic *O. palustris*. However, the morphological distinctiveness and morphometric separation of *peninsulae* that we observed are substantial and instead portray a species that evolved in situ, isolated appreciably longer from the mainland distribution of *Oryzomys* than a recent anthropogenic introduction would suggest.

The phenetic linkage of *O. couesi mexicanus* and *O. peninsulae* offers a preliminary kinship hypothesis to be tested with other data, and two biogeographic scenarios deserve consideration in reconstructing the latter's relict distribution. *Oryzomys peninsulae* may have differentiated from an ancestral stock whose distribution once covered the Baja Peninsula, extreme southwestern United States, and western Mexico. Several rodent species or species complexes today exhibit a similar distributional pattern (e.g., see ranges in Lawlor, 1983: appendix 10), suggesting that Pleistocene climatic changes and subsequent range contraction could have isolated

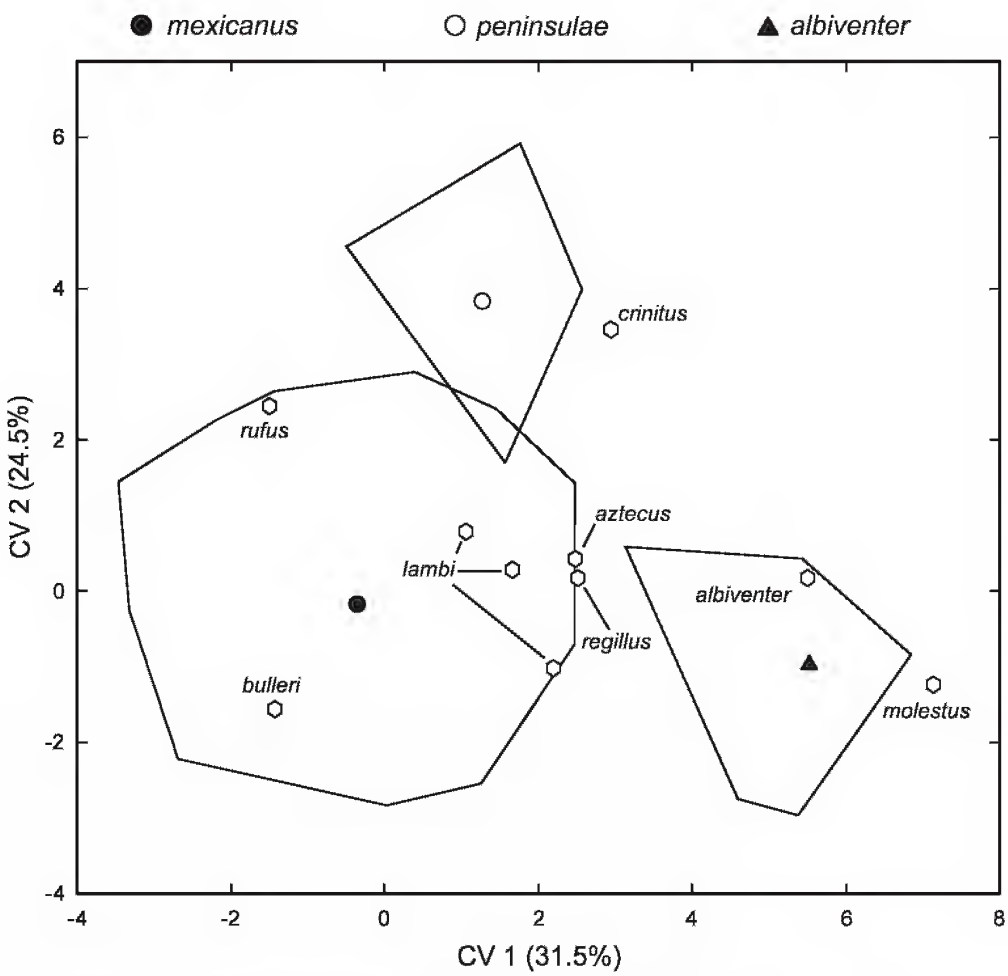

Fig. 6. Dispersion of type specimens of *Oryzomys* named from western Mexico based on a posteriori classification using discriminant coefficients extracted from 10-group discriminant function analysis of *albiventer*, *couesi mexicanus*, and *peninsulae*. Minimum convex polygons enclose individual scores around the group centroid (or grand centroid in the case of *couesi mexicanus*). See text for discussion.

an *Oryzomys* population at the tip of the peninsula. The extension of *O. couesi mexicanus* along the coastal plain in western Mexico, as far north as west-central Sonora (fig. 7), further intimates the former continuity of *Oryzomys* populations on the mainland surrounding the Sea of Cortez.

Alternatively, *O. peninsulae* may have originated when the southernmost cape region of the Baja Peninsula was positioned as an island approximate to the Nayarit-Jalisco coast in the late Miocene (Carreño and Helenes, 2002). Geologic and tectonic evidence indicates that northwestward rifting (beginning approximately 5.5 million years ago) and accelerated seafloor spreading (beginning approximately 3.5 million years ago) eventually brought the insular cape block to its present peninsular terminus, a geological nonconformity demarcated by the Isthmus of La Paz. The biotic legacy of the former juxtaposition of the southern cape block and west-central Mexico is suggested by the current distributions of certain plants and birds (Cody and Velarde, 2002; Cody et al., 2002). Phylogeographic analysis, using ancient DNA, may disclose sufficiently fine-scale genetic affinities to choose among these or other biographic scenarios.

TABLE 5

Measurements[a] (mm), Sex, and Age of Type Specimens of the *Oryzomys couesi* Group in Western Mexico

(Y, A, and O = young, full, or old adult age class, respectively. Variable abbreviations are defined in Materials and Methods.)

	O. albiventer		*O. nelsoni*	*O. peninsulae*	*O. couesi mexicanus*				*O.* c.f. *couesi*		
	albiventer USNM 82236	*molestus*[b] FMNH 8667	*nelsoni* USNM 89200	*peninsulae* BMNH 98.3.1.107	*mexicanus* AMNH 2650/2128	*bulleri* AMNH 8359/6663	*rufus* USNM 91404	*lambi*[c] UCLA topotypes	*crinitus* USNM 50182	*aztecus* USNM 51173	*regillus* USNM 125945
Sex	M	M	M	M	M	M	F	—	M	M	M
Age	A	O	A	A	A	Y	O	—	Y	Y	A
TOTL	288	325	342	298	249	242	250	226–229	307	290	305
TL	153	170	190	190	142	127	136	111–116	161	154	169
HFL	37.5	38	38	34	30	27	28	29–30	37	35	36
EL	—	15	—	18	13	11	—	17	—	—	—
ONL	32.7	36.1	37.7	33.8	—	28.0	28.1	30.2–30.4	32.6	32.3	33.5
ZB	17.9	19.4	18.6	18.3	—	14.9	15.9	15.9–16.5	17.0	16.9	18.2
BBC	13.7	14.1	13.3	13.2	12.6	12.7	12.2	12.1–12.4	13.4	13.0	13.6
BOC	7.2	7.7	7.2	—	—	6.4	6.4	6.7–6.8	6.9	7.2	7.2
DBC	10.2	10.6	9.9	—	—	8.7	9.3	8.8–8.9	10.6	9.9	10.1
IOB	5.0	5.5	5.5	5.2	4.7	4.5	4.8	4.6–4.7	5.0	5.0	5.0
LR	10.6	11.8	12.4	9.7	—	8.9	8.6	9.6–9.8	10.3	10.4	10.9
BR	6.4	7.2	7.2	7.1	6.3	5.1	5.7	5.8–6.1	6.5	6.3	6.9
DR	7.3	8.1	8.7	—	—	5.9	6.5	6.5–6.6	7.3	7.2	7.5
LIF	6.9	7.8	6.9	7.0	6.4	5.3	6.3	6.0–6.3	7.0	6.7	6.7
BIF	2.6	2.2	2.4	2.9	1.5	1.8	2.3	2.1–2.4	2.8	2.6	2.5
LD	8.8	10.1	9.6	8.8	8.2	6.8	7.5	8.1–8.5	9.0	8.5	9.0
PPL	11.1	12.9	12.7	12.1	—	8.9	9.3	10.1–10.3	11.3	11.2	11.6
LBP	5.9	6.6	7.2	6.0	5.7	4.8	4.9	5.1–5.4	5.6	6.0	6.3
BBP	6.2	—	6.0	6.5	5.6	5.4	5.3	5.6–5.8	5.9	5.9	6.2
BZP	3.5	3.9	4.3	3.6	3.5	2.7	3.2	3.2–3.3	3.1	3.2	3.7
LAB	4.5	4.9	4.4	4.4	4.2	3.9	4.3	4.2–4.6	4.8	4.3	4.5
CLM	5.17	5.60	4.96	5.22	4.63	4.46	4.24	4.32–4.77	4.87	4.97	4.77
WM1	1.58	1.63	1.56	1.53	1.26	1.28	1.26	1.40–1.46	1.44	1.44	1.44
DI	2.01	2.02	2.43	—	2.07	1.76	1.74	1.76–1.89	1.84	—	1.95

a External measurements as obtained from skin tags or given in original descriptions; craniodental measurements taken by the authors.

b Craniodental measurements supplied by W.T. Stanley, FMNH.

c Based on three original topotypes identified in Burt's (1934) subspecies description (UCLA 51021, M, YA; UCLA 51026, F, YA; UCLA 51038, F, A).

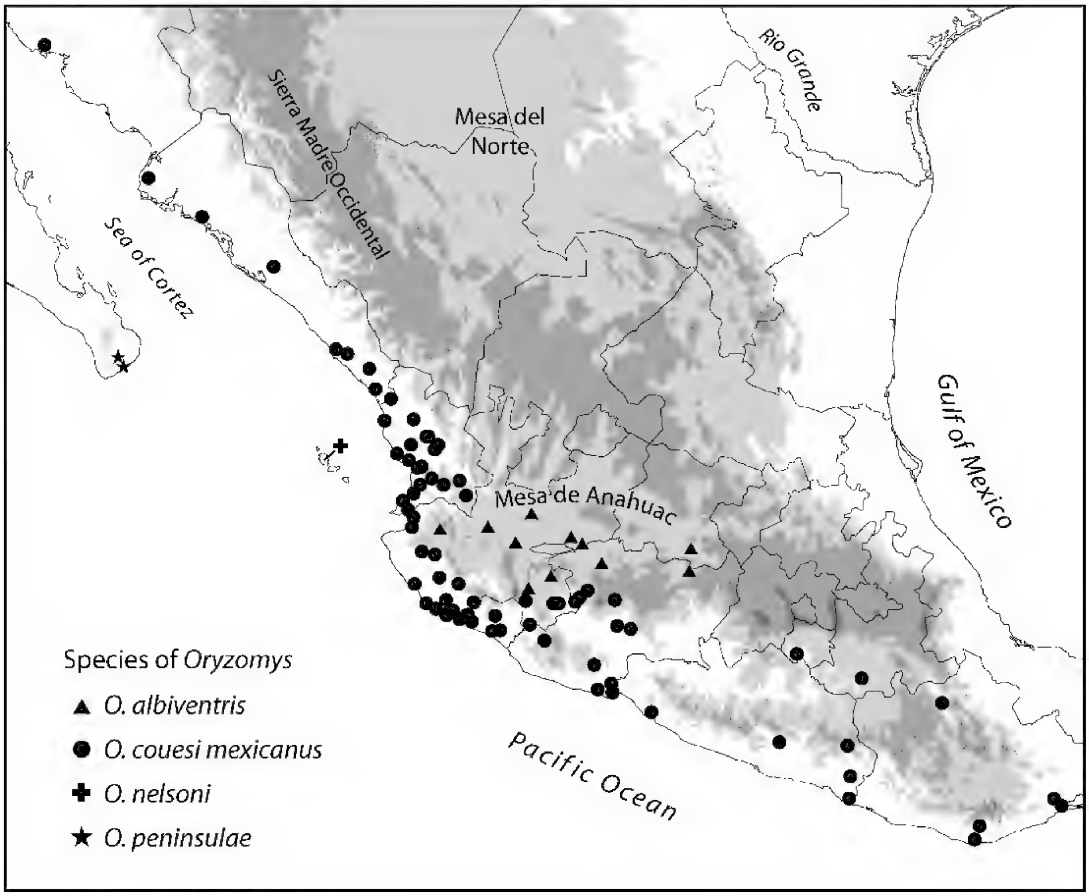

Fig. 7. Distribution of four species of *Oryzomys* here recognized in western Mexico, based on specimens examined by us. Gray shading represents the same elevation zones depicted in figure 1.

(2) The *Oryzomys* population that once inhabited Isla María Madre, the largest of the Tres Marías archipelago off Nayarit, has been accepted as a species by most authors since Merriam (1898) first described it as *O. nelsoni*. In spite of the small sample size (only four specimens known), the differentiation of *O. nelsoni* is sharply circumscribed from mainland forms and sustains its continued recognition as a species, following Merriam (1901) and Goldman (1918) and contra Hershkovitz (1971). In retaining *nelsoni* as a species, Goldman (1918) considered it to be closely allied to the nearest mainland form, *O. couesi mexicanus*. However, by its size, *O. nelsoni* invites careful comparison with *O. albiventer*, a species whose distribution is currently confined to the interior plateau region of west-central Mexico (fig. 7), removed from the coastal lowlands where the progenitor of the island species must have once occurred. The two were paired as the phenetically most similar OTUs in all multivariate analyses of craniodental variables (figs. 4, 5), and this linkage provides a working hypothesis of relationship to be tested with other data. *Peromyscus madrensis*, another rodent endemic of the Tres Marías Islands, was apparently isolated early during the radiation of the *P. boylii* species group (Tiemann-Boege et al., 2000). In like manner, perhaps *O. nelsoni* represents an old lineage within the diversification of western Mexican *Oryzomys*, diverging from the common ancestor that also gave rise to *O. albiventer*.

(3) We elected a conservative course and retained *mexicanus* Allen as a subspecies of *O. couesi* in lieu of the detailed analyses and

Fig. 8. Dorsal (upper row) and ventral (lower row) cranial views (ca. 2 ×) of adult *Oryzomys* representing species here recognized from western Mexico: **A**, *O. albiventer* (USNM 82240, ONL = 33.8 mm), a young adult male from Jalisco, Ameca, 4000 ft; **B**, *O. nelsoni* (USNM 89201, ONL = 34.6 mm), an adult female from Nayarit, Isla María Madre, 800 ft; **C**, *O. peninsulae* (USNM 146610, ONL = 32.3 mm), a young adult male from Baja California Sur, San José del Cabo; **D**, *O. couesi mexicanus* (USNM 509418, ONL = 32.2 mm), a young adult male from Nayarit, 1 mi S Cuautla, near sea level.

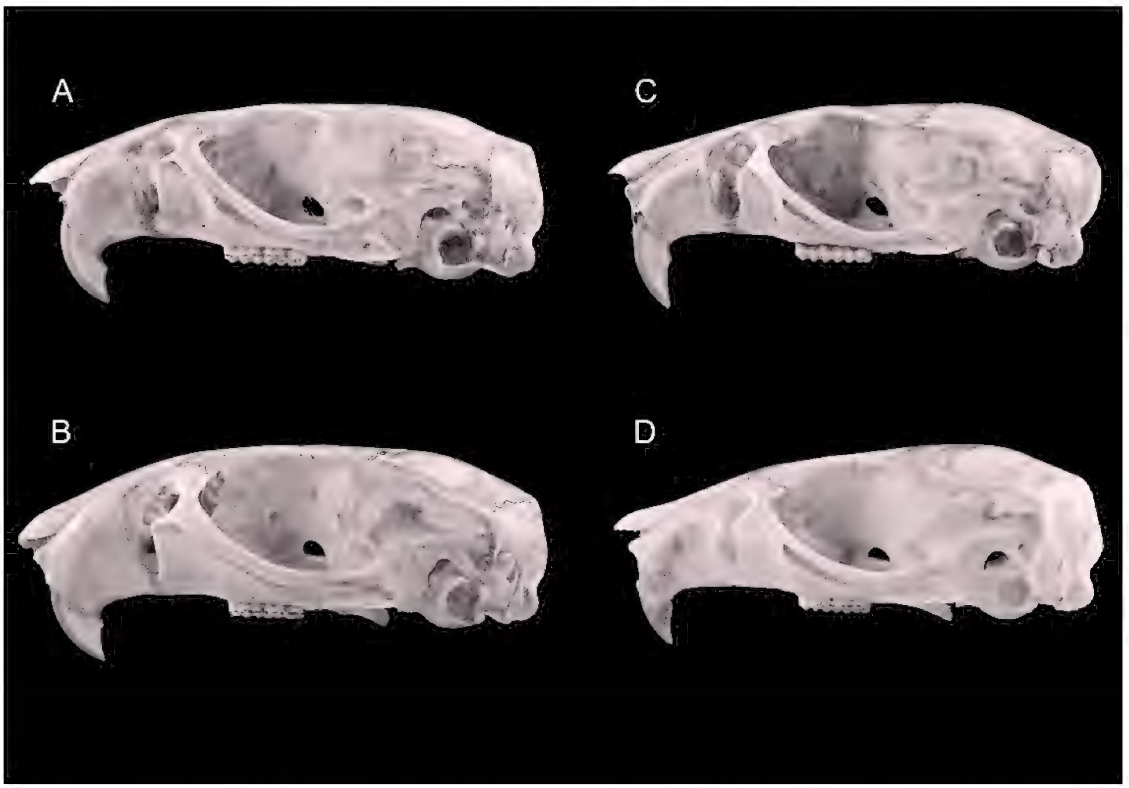

Fig. 9. Lateral cranial views (ca. 2 ×) of the same specimens adult *Oryzomys* illustrated in figure 8: **A**, *O. albiventer*; **B**, *O. nelsoni*; **C**, *O. peninsulae*; **D**, *O. couesi mexicanus*.

broader geographic canvas required to clarify its status. Visual comparisons of skins and skulls suggested that, among the four species in western Mexico, examples of *mexicanus* most closely resemble those of *O. couesi* proper, whose type locality is Coban, Guatemala. Recent studies of *Sigmodon "hispidus"* and *Peromyscus "boylii"* cast suspicion on such a conclusion: subspecies distributed along the western versus eastern versants of Mexico in those so-called species have been demonstrated to be distinct from one another (see above references). In particular, the distribution of *O. couesi mexicanus* is extensively congruent with that of *Sigmodon mascotensis* (Carleton et al., 1999), its range penetrating the interior along the basin of the Río Balsas and following the coastal plain to the Isthmus of Tehuantepec. In this case, however, examples of the large-bodied *S. mascotensis* are readily distinguishable from the smaller *S. toltecus* where their ranges approach one another in the region of the isthmus (Carleton et al., 1999; Peppers and Bradley, 2000). No such morphological dichotomy is apparent to us based on inspection of *O. couesi* specimens from the eastern lowlands of Mexico, the Isthmus of Tehuantepec, and Guatemala, including those that belong to the currently recognized subspecies *couesi* and *zygomaticus* (e.g., Hall, 1981). Other data sources and a broader geographic perspective are needed, one that stresses additional sampling in the Isthmus of Tehuantepec where *couesi mexicanus* and *O. c. couesi* are thought to intergrade (Goldman, 1918; Hall, 1981). Acquisition of topotypic material from the type localities of the several forms in eastern and southern Mexico placed in full synonymy under *O. c. couesi—jalapae* Allen and Chapman (1897), *jalapae rufinus* Merriam (1901), *jalapae apatelius* Elliot (1904), *goldmani* Merriam (1901), *teapensis* Merriam (1901)—may prove critical.

Farther south, the status and relationships of several other epithets will bear on delim-

iting the southern distributional occurrence of *O. couesi* proper. Jones and Engstrom (1986) considered *richmondi* Merriam (1901), whose type locality is in southeastern Nicaragua (Zelaya, 50 mi above Bluefields), to be another synonym that is inseparable from *O. couesi couesi*. Our examination of that type (USNM 36340/48705) indicates that it is an example of *O. couesi*, but evaluation based on denser geographic sampling is necessary before one might comment on subspecific divisions. Another *Oryzomys* described from southeastern Nicaragua (Zelaya, 7 mi below Rama) is the enigmatic *O. dimidiatus* Thomas (1905), known by only two specimens, but investigators who have examined the taxon have retained it as a valid species (Genoways and Jones, 1971; Jones and Engstrom, 1986; Musser and Carleton, 1993; Sánchez et al., 2001). In reporting the rediscovery of *O. gorgasi* Hershkovitz (1971), Sánchez et al. (2001) confirmed its distinction from other forms described from southern Central America, including *dimidiatus* Thomas (1905), *gatunensis* Goldman (1912), and *richmondi* Merriam (1901), the latter two taxa now placed under *O. couesi*. The distribution of *O. gorgasi* plausibly extends into southern Central America, and museum series from this region should be reexamined with the fresh perspective supplied by Sánchez et al. (2001).

(4) Within his arrangement of *O. couesi*, Goldman (1918: 37) identified a complex of related subspecies from central Mexico: "It [*O. c. crinitus*] is closely allied to the other forms inhabiting river valleys of the plateau region of Mexico—*O. c. aztecus*, *O. c. albiventer*, and *O. c. regillus*." As argued above, we acknowledge *O. albiventer* to be specifically distinct from *O. couesi mexicanus*, the form distributed along coastal plain and lower mountain slopes in western Mexico (fig. 7). Of the four taxa described from interior uplands, *O. albiventer* Merriam (1901: 279) is an older name than *regillus* Goldman (1915) and has page priority over *crinitus* Merriam (1901: 281) and *aztecus* Merriam (1901: 282). Evidence for the synonymy of these forms with *O. albiventer* is so far unpersuasive, however.

Post hoc classification of the type specimens of the latter three taxa, based on 19 craniodental variables, associates them with *O. couesi mexicanus* (*aztecus* and *regillus*) or with *O. peninsulae* (*crinitus*), not with *O. albiventer*. The holotypes and type series of *aztecus* and *regillus* consist of large individuals whose dimensions measure at the upper limits of variation observed within typical *O. couesi mexicanus* (compare tables 2 and 5), and it is zoogeographically plausible that these names simply apply to more robust populations of the same species where they occupy higher elevations. Whether they represent yet another species within the *O. couesi* group must await improved sample sizes and additional data sources to discern broader patterns of variation and critically decide their status. We do not accept that populations represented by the type of *crinitus*, described from over 2000 m in the Valley of Mexico, and the series of *peninsulae*, described from near sea level at the tip of Baja California, form one and the same biological species. As in the case of *aztecus* and *regillus*, we view these discriminant-function results as indicative of taxonomic problems in need of resolution and the probable existence of greater species diversity than offered by our predefined OTUs. The recent photograph of a large, long-tailed *Oryzomys* from the Distrito Federal (Medellín and Medellín, 2006: 710), verifies that populations referable to *crinitus* Merriam still persist in the Valley of Mexico and invite elucidation of their systematic relationships.

(5) *Oryzomys fulgens* Thomas (1893) is a little-known and overlooked taxon, but clarification of its status will prove pivotal in deciding nomenclatural issues that concern *albiventer* and the other upland taxa, especially *crinitus*. Thomas described *fulgens* based on one of the three specimens originally used by Alston (1876) in his characterization of *Hesperomys couesi*. In doing so, Thomas selected a lectotype for *H. couesi* (specimen "a" = BMNH 75.2.26.15) and fixed its type locality (Coban, Guatemala). The type locality of the specimen that he designated as the type of *O. fulgens* ("b" = BMNH 70.6.20.3), collected by the French naturalist Adolphe Boucard (1839–1905), was given only as "Mexico, exact locality unknown." Thomas supposed that it originated from "southern Mexico, probably in or

near the Valley of Mexico," and his supposition about the source of Alston's specimen "b" has been repeated in the subsequent taxonomic literature on *Oryzomys* (Merriam, 1901; Goldman, 1918; Miller and Kellogg, 1955; Hall, 1981). No one has since offered a formal restriction of the type locality, however. In spite of the possible origin of *fulgens* from the Valley of Mexico, Merriam (1901) proceeded to name another species, *O. crinitus*, from the same region (Distrito Federal, Tlalpan) and suspected that it "will prove only a subspecies of *fulgens*." Merriam had not examined the type of *fulgens* but based his impression of their close similarity on Thomas' description, which he quoted in full. Apparently the indeterminate type locality of *fulgens* persuaded Merriam to name *crinitus* as a full species based on a well-prepared specimen newly collected by Nelson and Goldman, conveniently at hand, and with undoubted provenience.

When nearly all Middle American forms of *Oryzomys* were viewed as races of the older taxa *O. couesi* (Alston, 1876) or *O. palustris* (Harlan, 1837), the imprecise geographic source of the junior name *fulgens* Thomas (1893) was nomenclaturally inconsequential. Its possible senior status among *Oryzomys* taxa named from uplands in interior Mexico now invites careful archival research on Boucard's travels to see whether a definite type locality can be established and the name can be critically applied to *Oryzomys* populations. Having satisfied that crucial step, the relationship of *fulgens* to *albiventer*, *crinitus*, and *aztecus* can be addressed and synonymies allocated if appropriate.

(6) Individuals of *Oryzomys* commonly inhabit coastal wetlands (Sharp, 1967; Wolfe, 1982, 1985), are adept swimmers (Svihla, 1931; Hamilton, 1946; Esher et al., 1978), and are known to emigrate between near-shore islands (Forys and Dueser, 1993). Their semiaquatic habits and ecological preference readily explain the common presence of *Oryzomys* on continental-shelf islands and perhaps the one oceanic occurrence (*O. antillarum* on Jamaica). Several of these peripheral isolates acquired species-group epithets, all of which were hastily reallocated as subspecies of the all-inclusive *O. palustris* (Hershkovitz, 1971; Hall, 1981). As demonstrated for *O. antillarum* by Morgan (1993) and documented herein for *O. nelsoni* and *O. peninsulae*, however, the differentiation of these insular and peninsular forms is appreciable and contradicts their continued maintenance under the one mainland species *O. couesi*. Other insular and peninsular forms (*azuerensis*, *cozumelae*, and *gatunensis*) now retained within *O. couesi* similarly deserve objective assessment of their status. The generic assignment of the subfossil form described from Curaçao (McFarlane and Debrot, 2001), a continental-shelf island in the Netherlands Antilles, and its possible synonymy with *O. gorgasi* also warrant attention (see comments in Musser and Carleton, 2005: 1148, and Weksler et al., 2006: 4).

CONSERVATION NOTES: *Oryzomys nelsoni* is known by only four specimens of the original type series (Merriam, 1898), obtained by Nelson and Goldman from María Madre Island in May 1897, and is considered extinct (Ceballos et al., 2002; Alvarez-Castañeda and Méndez, 2003; IUCN, 2006). The specimens were collected in moist herbaceous vegetation surrounding springs located on the upper slopes (~ 245 m) of María Madre (Nelson, 1899a, 1899b), the largest of the Tres Marías Islands. No other dedicated inventory of small mammals occurred until Don E. Wilson led a Biological Survey field team to the Tres Marías in March 1976. Wilson and colleagues located the area described by Nelson where *O. nelsoni* had been discovered but collected only *Rattus rattus*; Wilson (1991) inferred that the abundant presence of the commensal may have contributed to the extinction of *O. nelsoni*. Another Tres Marías endemic rodent, *Peromyscus madrensis*, was recovered in moderate numbers on Isla María Madre along with *Rattus rattus* (Carleton et al., 1982; Wilson, 1991).

Current evidence holds little promise that populations of *O. peninsulae* persist. The form is documented from only two localities, Santa Anita and San José del Cabo, in southernmost Baja California. The original series (6 specimens) from Santa Anita, the type locality (Thomas, 1897), was collected by Dane Coolidge (1873–1940), a freelance field collector and writer, in May 1896. The 15 USNM specimens from San José del Cabo

were obtained by Nelson and Goldman in January 1906; the companions afterward traveled to Santa Anita but failed to collect any topotypic examples of *O. peninsulae*. The localities are about 13 km apart and both were situated along the Río San Jose, a permanent river around the turn of the century that flowed through the predominantly arid landscapes in southern Baja California (Nelson, 1922; Goldman, 1951). Goldman (1918: 46) reported that "The range of the species seems to be centered in the marshes near the mouth of the San José River at San José del Cabo, extending a few miles inland along the course of the stream," and that "The neighboring coast is extremely arid and unsuitable for habitation by an *Oryzomys*." Subsequent habitat changes over the latter half of the 20th century in southern Baja California have been dramatic and would be inimical for a semiaquatic rodent tied to such a precarious ecological niche. The river no longer exists, having been sapped dry for irrigation projects, and the marshy lagoon at its mouth in San José del Cabo is polluted commensurate with development of the shoreline for tourism (Alvarez-Castañeda, 1994). Two deliberate attempts to rediscover *peninsulae* in the late 1900s proved unsuccessful: Michael A. Bogan and a Biological Survey field team visited San José del Cabo for one intensive night of collecting in 1979, and Ticul Alvarez-Castañeda (1994) surveyed habitats in and around both Santa Anita and San José del Cabo several times over 1991–1993. The vulnerability of *O. peninsulae* has been obscured by its confusion under *O. couesi*, a species viewed as broadly distributed and accordingly classified as Lower Risk—least concern (IUCN, 2006). The conservation status of *O. peninsulae* must be considered critically endangered, if not extinct, in view of its lack of documentation in over a century, its restricted geographic occurrence, and the environmental deterioration that has befallen its preferred habitat.

Of the two remaining species we identify within western Mexico, populations of *O. couesi mexicanus* appear to deserve the IUCN designation of "Lower Risk—least concern." Large series of this species have been documented within the latter 1900s, e.g., from lowlands of Nayarit, Colima, and Jalisco. On the other hand, we encountered few examples of *O. albiventer* in North American collections, only 26 specimens representing 11 localities. Most of these represent material collected by Nelson and Goldman in Jalisco over the years 1897–1903, supplemented by scattered specimens obtained by KU field crews over the years 1949–1969. The distribution of *O. albiventer* largely conforms to the sloping plateau, ca. 1200–1900 m, surrounding Lago de Chapala and its greater drainage basin. Given its hydrographic advantages and more mesic climate, the region has long attracted large-scale agricultural development, and Goldman (1951) described the dramatic environmental changes that had transpired between his early (1902–1903) and later visits (1926, 1935) to the area (see especially accounts for La Barca and Ocotlán). Although populations must be highly fragmented, we believe that the species survives in pockets of appropriate habitat. Efforts should be devoted to surveying the current status of *O. albiventer*, including refinement of its distribution based on vouchered specimens contained in Mexican collections. This refinement necessarily involves resolution of its relationship to the other forms described from central Mexico (see topics 4 and 5 above).

TAXONOMIC SUMMARY

Synonymies are presented below for the four species of *Oryzomys* recognized in western Mexico and trace their earliest identification and first subsequent usage in other name combinations. Emended diagnoses are presented for those two (*O. albiventer* and *O. peninsulae*) that have long been confused with *O. palustris* or *O. couesi* (e.g., fide Goldman, 1918, and Hall, 1981). We regard the status of *aztecus* Merriam, *crinitus* Merriam, and *regillus* Goldman from central Mexico as unresolved and provisionally retain them within *O. couesi* sensu lato (appendix 1). Specimens examined include all individuals personally seen and identified by us. An emended diagnosis is also given for the phylogenetically restricted construct of *Oryzomys*. See Weksler et al. (2006) for character traits and diagnoses of the new genera that have been removed from the

polyphyletic shell that so long characterized "*Oryzomys*" in its traditional usage (Merriam, 1901; Goldman, 1918; Hall, 1981).

Oryzomys Baird, 1857

Mus, Harlan, 1837: 385 (part, description of *palustris*).

Arvicola, Bachman, 1854 [in Audubon and Bachman, 1846–1854]: 214 (part, description of *oryzivora*).

Hesperomys (*Oryzomys*) Baird, 1857: 482.

Oryzomys, Allen, 1890: 187 (first usage as genus).

TYPE SPECIES: *Mus palustris* Harlan, 1837, by original designation.

EMENDED DIAGNOSIS: A clade of medium-sized oryzomyine species (Cricetidae: Sigmodontinae: Oryzomyini) characterized, in combination, by: supraorbital ridging well developed and interorbital shape cuneate; incisive foramina long, extending to or between the alveoli of the M1s; bony palate long, projecting behind the posterior margins of M3s, and posterolateral palatal pits conspicuous and internally perforated; ectotympanic bulla medium-sized, revealing ventral-medial wedge of the periotic; zygomatic plate broad, forming a moderately deep notch, and zygomatic arches sturdy, with small but consistently formed jugal; interparietal small and narrow, about half as wide as the caudal border of parietals; alisphenoid strut absent; carotid arterial circulatory pattern derived, lacking supraorbital and infraorbital branches (sphenofrontal foramen and squamosal-alisphenoid groove absent, stapedial foramen absent or minute, posterior opening to alisphenoid canal irregularly formed or occluded). Molars pentalophodont (mesolophs/ids well developed) and cuspidate, cusps bunodont with lingual and labial series unevenly terraced; anterocone/id broad, anteromedian flexus/id absent, anteroloph discrete and well formed; satellite rootlets present on M1 (4-rooted) and m1 (3–4-rooted). Eight mammae present (pectoral, postaxial, abdominal, and inguinal pairs); pedal digits 1 and 5 notably shorter than central three; ungual tuft of hairs sparsely developed, covering less than half of the nail; plantar surface squamate and pads small, hypothenar pad minute or absent.

DISTRIBUTION: Palustrine, lacustrine, and riverine habitats in the southeastern United States, throughout much of Mexico and Central America, to northwestern South America (western Colombia and northwestern Venezulela), including many continental-shelf islands.

CONTENTS: ***albiventer*** Merriam, 1901 (including *molestus* Elliot, 1903); ***antillarum*** Thomas, 1898; ***couesi*** Alston, 1876 (including *apatelius* Elliot, 1904; *aquaticus* J.A. Allen, 1891; *aztecus* Merriam, 1901; *azuerensis* Bole, 1937; *bulleri* J.A. Allen, 1897; *cozumelae* Merriam, 1901; *crinitus* Merriam, 1901; *fulgens* Thomas, 1893; *gatunensis* Goldman, 1912; *goldmani* Merriam, 1901; *jalapae* J.A. Allen and Chapman, 1897; *lambi* Burt, 1934; *mexicanus* J.A. Allen, 1897; *peragrus* Merriam, 1901; *pinicola* A. Murie, 1932; *regillus* Goldman, 1915; *richardsoni* J.A. Allen, 1910; *richmondi* Merriam, 1901; *rufinus* Merriam, 1901; *rufus* Merriam, 1901; *teapensis* Merriam, 1901; *zygomaticus* Merriam 1901); ***dimidiatus*** Thomas, 1905 ; ***gorgasi*** Hershkovitz, 1971; ***nelsoni*** Merriam, 1898; ***palustris*** Harlan, 1837 (including *argentatus* Spitzer and Lazell, 1978; *coloratus* Bangs, 1898; *floridanus* Merriam, 1901; *natator* Chapman, 1893; *oryzivora* Bachman, 1854 [in Audubon and Bachman, 1854]; *planirostris* Hamilton, 1955; *sanibeli* Hamilton, 1955; *texensis* J.A. Allen, 1894); ***peninsulae*** Thomas, 1897.

REMARKS: In the early taxonomic literature on North American forms (Merriam, 1901; Goldman, 1918), Baird's *Oryzomys* was broadly conceived and included species groups and subgenera now removed to separate genera (Gardner and Patton, 1976; Carleton and Musser, 1989; Weksler, 2003, 2006; Weksler et al., 2006). The phylogenetically reified understanding of *Oryzomys* corresponds to the association of species placed in the *palustris-mexicanus* or *palustris* group, as designated, respectively, by Merriam (1901) and Goldman (1918). Thus, *O. albiventer*, *O. couesi mexicanus*, *O. nelsoni*, and *O. peninsulae* share with *O. palustris* those derived conditions that characterize the strict concept of *Oryzomys* (Carleton and Musser, 1989; Carleton and Olson, 1999; Sánchez et al., 2001) and that were amplified to infer the phylogenetic position of the genus within the oryzomyine radiation (Weksler, 2006).

The four western Mexican species further exhibit the trenchant characteristics of the *couesi* section within the *O. palustris* group, as denoted by Goldman (1918: 20) based on several pelage and cranial traits. In the *palustris* section, the pelage color is predominantly grayish brown, with long glistening guard hairs conspicuously overtopping the body fur; the pelage color is generally reddish brown, with the guard hairs only slightly longer than the body fur in the *couesi* section. Spacious, oval sphenopalatine vacuities perforate the walls of the mesopterygoid fossa, exposing much of the presphenoid bone in specimens of *O. palustris* (e.g., see character 36: state 0, as per Weksler, 2006); in forms of the *couesi* section, sphenopalatine vacuities are absent or weakly expressed as short, narrow slits near the basisphenoid-presphenoid suture (character 36: states 1 and 2, as per Weksler, 2006). Other differences reinforce Goldman's perception of a division. *Oryzomys couesi* and the western Mexican species all possess a small, circular sphenopalatine foramen in contrast to the larger, ovate shape of the foramen as observed in skulls of *O. palustris*. Schmidt and Engstrom (1994) drew attention to the utility of this contrast in separating crania of *O. palustris texensis* and *O. couesi aquaticus* where their populations overlap along coastal Texas, but the contrast holds between *O. palustris* and the four species in western Mexico as well. We noticed that the two sections also differ in the development of the anterolabial cingulum on the lower third molar: consistently present and forming a distinct ledge in the *couesi* section; absent or represented as a short spur in members of the *palustris* section (see Carleton and Musser, 1989: 44–45, for description and illustration of the condition in *O. palustris*). Plantar pads of the hindfoot are small in species of *Oryzomys* compared with many other oryzomyines, and the hypothenar pad is typically absent in *O. palustris* or tiny if present (Carleton and Musser, 1989; Weksler, 2006). A hypothenar pad is consistently present in all members of the *couesi* section for which we could ascertain its condition, its size slightly smaller than interdigital pads 1 and 4. Weksler (2006) scored incipient webbing as present between pedal digits 2–3 and 3–4 in his sample of *O. palustris* but absent in that of *O. couesi*, and Sánchez et al. (2001) indicated that such webbing also characterized *O. dimidiatus* and *O. gorgasi*. Based on examinations of the hind feet on dried skins and even fluid-preserved specimens of the taxa in western Mexico, we are uncertain about the condition of this trait. Certainly, webbing is not so obviously developed as in *O. palustris*, but slight webbing seemed to be present between digits 3–4 in some specimens. This character definition and variation should be critically reviewed within *Oryzomys* to better understand its taxonomic significance.

In summary, the *palustris* and *couesi* "sections" of Goldman's *palustris* group are sufficiently characterized morphologically to maintain them as the *palustris* and *couesi* species groups within the genus *Oryzomys* as now phylogenetically diagnosed. For the character variation summarized above, the *palustris* group displays more derived conditions and may possess more semiaquatic adaptations than the *couesi* group. Only *O. palustris* is currently recognized as a valid species within the *palustris* group; the principal alpha systematic uncertainty involves the status of *argentatus* Spitzer and Lazell (1978), a form described from the Florida Keys that has been treated as species or subspecies (see Musser and Carleton, 2005, for review). The other seven species fit with the *couesi* group, but as underscored by our findings in western Mexico, comprehension of species limits warrants additional research.

Oryzomys albiventer Merriam, 1901

Oryzomys albiventer Merriam, 1901: 279. *Type locality:* Mexico, Jalisco, Ameca, 4000 ft; *holotype*: USNM 82236 (skin and skull), a male collected 6 February 1897 by E.W. Nelson and E.A. Goldman.

Oryzomys couesi albiventer, Goldman, 1918: 38 (name combination, allocated as valid subspecies).

Oryzomys palustris albiventer, Hall, 1960: 173 (name combination, listed as valid subspecies).

Oryzomys molestus Elliot, 1903: 145. *Type locality*: Mexico, Jalisco, Ocotlán, 5000 ft; *holotype*: FMNH 8667 (skin and skull), a male collected June 1901 by F.E. Lutz (not examined).

Oryzomys couesi albiventer, Goldman, 1918: 38 (*molestus* allocated as full synonym, invalid as subspecies).

Oryzomys palustris albiventer, Hall, 1981: 609 (*molestus* listed as full synonym, invalid as subspecies).

EMENDED DIAGNOSIS: A species of the *O. couesi* group characterized by a combination of large size (HFL ≈ 34–38 mm), tail relatively and absolutely long (TL ≈ 140–170 mm), skull heavily constructed (ONL ≈ 31–34 mm), and molars correspondingly robust (CLM ≈ 5.0–5.4 mm).

DISTRIBUTION: Central and eastern Jalisco, southern Guanajuato, and northern Michoacán at intermediate elevations, 1200–1800 m (fig. 7).

REMARKS: *Oryzomys albiventer* is a large, brightly colored species with a long tail. Merriam's (1901) key diagnostic feature, "underparts white," and consequent choice of the specific name are somewhat misleading. The basal portion of ventral hairs is pale gray and the distal half a pure white in the type series from Ameca. The white tips do not obscure the basal gray and, to us, create a general effect of pale gray to grayish-white underparts. In the specimens from Ocotlán, the gray bases are more prominent and the underparts appear medium gray. Other aspects of Merriam's description are accurate, notably the large skull and long and wide molar rows which he emphasized in his comparisons with nearby species. Goldman (1918) repeated these salient contrasts in his rearrangement of *albiventer*, *mexicanus*, and *regillus* as subspecies of *O. couesi* in western Mexico.

Goldman (1918) reallocated *molestus* Elliot (1903) as a full synonym of Merriam's (1901) *albiventer* (then a subspecies of *O. couesi*), and we concur with their synonymy. Elliot based his new species on a single specimen, but four other individuals in USNM from Ocotlán, the type locality of *molestus*, conform to his description. The type specimen of *molestus* is a strikingly large individual (table 5), but it is, as noted by Goldman, an old adult and a male. Measurements of the type fit within the size range of *O. albiventer* as we understand the species, albeit at or toward the upper limits for most variables; still, discriminant-function analysis decidedly assigned the type to the *albiventer* OTU. Two specimens from localities in northern Michoacán (Zamora and Querándaro), which Goldman (1918) referred to *O. c. regillus*, are here considered examples of *O. albiventer* proper.

Although the distributional limits of *O. albiventer* require further documentation, the species so far appears to be endemic to the Mesa de Anáhuac, a small inland plateau (1200–1900 m) that is enclosed by southern ranges of the Sierra Madre Occidental and by the Transverse Volcanic Range. Characterized by a subhumid climate and subtropical vegetation, the region corresponds to one of the five zoogeographic zones that Guerrero Vázquez et al. (1995) identified within Jalisco.

SPECIMENS EXAMINED: Mexico, *Guanajuato*: Salvatierra, 5775 ft (KU 66597). *Jalisco*: Ameca, 4000 ft (USNM 82235–82246); 6 km NE Contla, 1310 m (KU 120611, 120612); 2 mi N and 0.5 mi W Guadalajara, 5200 ft (KU 31782, 31783); 27 mi S and 12 mi W Guadalajara (KU 31784); La Barca (USNM 129038); 2 mi SE Mascota, 5200 ft (KU 100509); Ocotlán, 5000 ft (USNM 120160–120163); 4 km W Tuxpan, 1380 m (KU 120613). *Michoacán*: Querándaro (USNM 50180); Zamora, 4000 ft (USNM 120308).

Oryzomys couesi mexicanus J.A. Allen, 1897

Oryzomys mexicanus J.A. Allen, 1897: 52. *Type locality*: Mexico, Jalisco, Tonila, Hacienda San Marcos, 3500 ft; *holotype*: AMNH 2650/2128 (skin and skull), a male collected 30 December 1889 by Audley C. Buller.

Oryzomys couesi mexicanus, Goldman, 1918: 33 (name combination, allocated as valid subspecies).

Oryzomys palustris mexicanus, Hall, 1960: 173 (name combination, listed as valid subspecies).

Oryzomys bulleri J.A. Allen, 1897: 53. *Type locality*: Mexico, Tepic [Nayarit], Valle de Banderas; *holotype*: 8329/6663 (skin and skull), a male collected 2 February 1893 by Audley C. Buller.

Oryzomys couesi mexicanus, Goldman, 1918: 33 (*bulleri* allocated as full synonym, invalid as subspecies).

Oryzomys palustris mexicanus, Hall, 1981: 610 (*bulleri* listed as full synonym, invalid as subspecies).

Oryzomys rufus Merriam, 1901: 287. *Type locality*: Mexico, Tepic [Nayarit], Santiago, 200 ft;

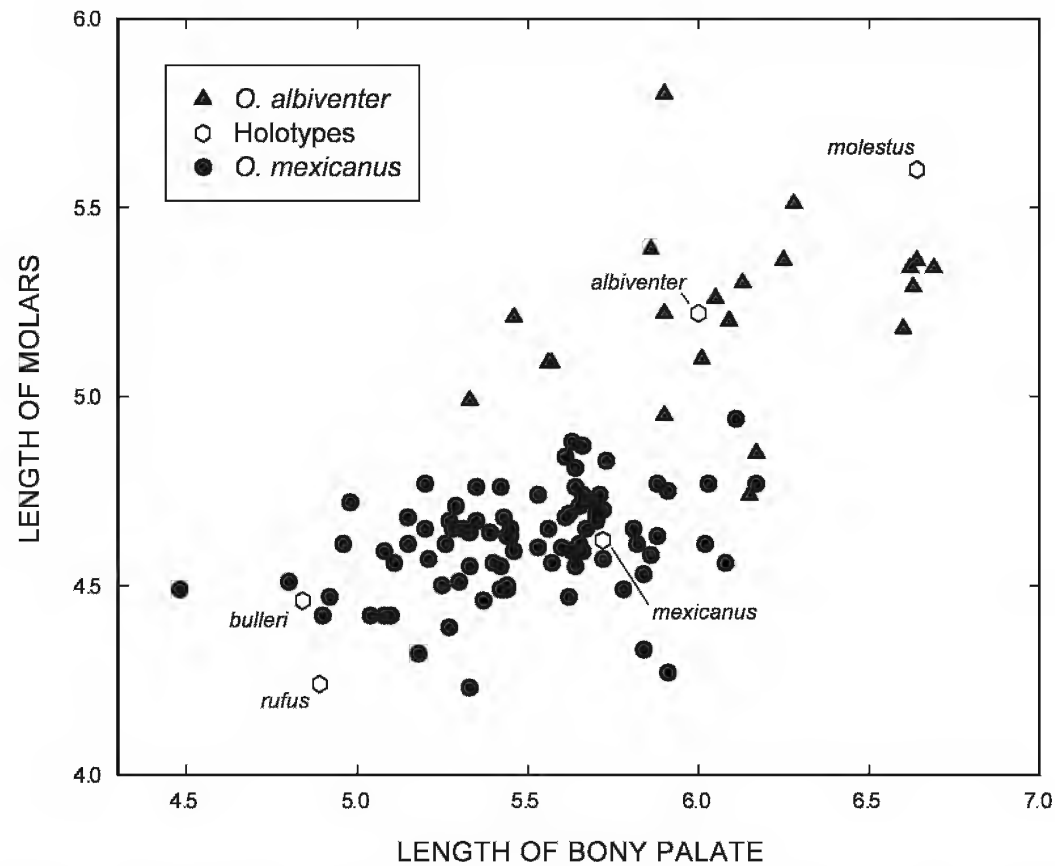

Fig. 10. Scatter plot of coronal length of molar rows versus length bony palate (in mm) for specimens of *O. albiventer* and *O. couesi mexicanus* from Jalisco. Values for type specimens of taxa described from Jalisco (*albiventer* Merriam, *mexicanus* Allen, *molestus* Elliot) and nearby Nayarit (*bulleri* Allen, *rufus* Merriam) are indicated.

holotype: USNM 91404 (skin and skull), a female collected 20 June 1897 by E.W. Nelson and E.A. Goldman.

Oryzomys couesi mexicanus, Goldman, 1918: 33 (*rufus* allocated as full synonym, invalid as subspecies).

Oryzomys palustris mexicanus, Hall, 1981: 610 (*rufus* listed as full synonym, invalid as subspecies).

Oryzomys couesi lambi Burt, 1934: 107. *Type locality*: Mexico, Sonora, San José de Guaymas; *holotype*: California Academy of Sciences 51024 (skin and skull), a female collected 20 January 1933 by C.C. Lamb (not examined).

Oryzomys palustris lambi, Hall, 1960: 173 (name combination, listed as valid subspecies).

DISTRIBUTION: Coastal plain and adjoining lower Pacific-facing slopes from central Sonora to southeastern Oaxaca; interior river valleys to central Michoacán, southern Morelos, southern Puebla, and northwestern Oaxaca (fig. 7); most localities from sea level to 1000 m, exceptional occurrence at 1525 m in the Sierra de Autlán, Jalisco.

REMARKS: J.A. Allen (1897) named *mexicanus* and *bulleri* as new species based on one specimen of the former and two of the latter. Although their type localities are relatively near one another in western Mexico, he differentiated *mexicanus* with respect to *O. palustris* and *bulleri* to *O. couesi* rather than to one another. Working with larger series and better geographic representation, Goldman (1918) recognized the fundamental similarity of Allen's taxa and adopted *mexicanus* as the subspecific epithet, with *bulleri* as full synonym, for the populations of smaller *Oryzomys* widely distributed along Pacific coastal plain. Although the damaged

skull of the type of *mexicanus* prevented its use in our morphometric analyses, bivariate scatterplots of measurable variables depict both *mexicanus* and *bulleri* as falling within the range of samples drawn from coastal plain (fig. 10), in contrast to those originating from the inland plateau region (i.e., *albiventer* and *molestus*).

Merriam (1901: 287) considered his new species *rufus*, based on a single specimen, to be "similar in general to *bulleri* but smaller and redder." The type specimen is a small individual (table 5) but falls within the variational sphere of the larger series from Nayarit and Jalisco, whether viewed from a univariate or multivariate perspective (figs. 6, 10). The contrasts that impressed Merriam can be largely attributed to the age and gender differences of the types of *bulleri* (young adult male) and *rufus* (old adult female) and the tendency of the pelage of aged *Oryzomys* to become more reddish. Again, we agree with Goldman's (1918) synonymy of *rufus* under *O. couesi mexicanus*.

The three topotypes of *lambi* Burt (1934) at hand generally resemble other examples of the *Oryzomys* species that inhabits coastal lowlands in western Mexico (e.g., fig. 6, table 5), here called *O. couesi mexicanus*, and we include it among the synonyms of this "subspecies." Our maintenance of a trinomial is pro forma in this instance because we cannot here resolve the larger issue of the taxonomic and distributional limits of *O. couesi* sensu stricto. The subspecific range of *lambi* is depicted as restricted to its type locality in west-central Sonora, whether as a race of *O. couesi* (Hall and Kelson, 1959; Alvarez-Castañeda and Cortés-Calva, 1999) or *O. palustris* (Hall, 1981). We note that certain specimens from northern Sinaloa (e.g., 2 mi E Costa Rica, 3 mi N Higueras) are larger than those from southern Sinaloa and farther south along coastal plain in Nayarit, Jalisco, and Colima, and may belong with Burt's *lambi*. Denser sampling in central Sinaloa and refined analyses are needed to determine the relationships of these populations and whether *lambi* deserves formal subspecific retention.

Goldman (1918) viewed the distribution of the subspecies *mexicanus* to adhere to Pacific coastal plain and contiguous foothills, a range conforming to his Arid Lower Tropical Zone (and Goldman, 1951) and essentially repeated in later taxonomic compendia of mammals (Hall and Kelson, 1959; Hall, 1981). However, specimens from certain localities that Goldman allocated to *aztecus* also represent *O. couesi mexicanus* proper in our judgment, and these reallocations extend its range into interior Mexico along the valleys of the Ríos Tepalcatepec and Balsas. A geographic range that covers coastal plain, Pacific-facing lower slopes of western sierras, and the Balsas Depression resembles other cricetid rodents found in western Mexico (e.g., *Sigmodon mascotensis*, *Hodomys alleni*, *Peromyscus perfulvus*, *Osgoodomys banderanus*) and presumably reflects a shared biogeographic history. The pattern is nearly exactly congruent to the biotic zone distilled from the distributions of the Mexican herpetofauna (Flores-Villela, 1993) but is not so precisely mirrored in those recognized in biogeographic syntheses of birds and mammals (Escalante Pliego et al., 1993; Fa and Morales, 1993).

Specimens Examined: Mexico, *Colima*: Armería, 200 ft (USNM 33284/45312–33285/45313, 33292/45320–33297/45325); 4 km S and 2 km W El Chavarín (CM 79555, 79556); Hacienda Magdalena, 1500 ft (USNM 33299/45327, 33300/45328); 5 mi N Manzanillo (KU 87515–87534); Paso del Río, 200 ft (UMMZ 100656–100669, 100689); 3 mi N Santiago (KU 87490–87492, 87653); 1 mi NE Santiago, 10 ft (KU 36867–36873); 2 km E Santiago (KU 87498); 3 km E Santiago (KU 87499–87514); 1 mi S and 4 mi W Santiago, 10 ft (KU 36874); 12 km W Santiago (KU 87493–87497). *Guerrero*: 5 km N Agua del Obispo, 3250 ft (KU 99899); 5.5 km N Agua del Obispo, 3400 ft (KU 99898); near Ometepec, 200 ft (USNM 71400–71405, 71419); Zihuatanejo Bay (UMMZ 80926, 80927, 80929, 80931); Petacalco, sea level (UMMZ 113850–113852); Tlalixtaquilla, 4200 ft (USNM 70277); 2 km SSE Zihuatanejo, Las Gatas (KU 35371–35379). *Jalisco*: 11 mi SW Autlán, 2000 ft (KU 105742); Sierra de Autlán, 5000 ft (UMMZ 95476, 95477); Cihuatlán, 15 ft (KU 109262–109265); 15 KM NW Cihuatlán (87454); Cuitzamala, 25 ft (KU 105743–105763); 2 km NW Emiliano Zapata, 20 m (KU 120615); Jilotlán de Los Dolores, 2400 ft (KU 111830, 111831); 8 mi E Jilotlán de Los

Dolores, 2000 ft (KU 111832–111837); 6 mi E Limón, 2700 ft (KU 103799); 2 mi S La Cuesta, 2400 ft (KU 111829); 2 mi N La Resolana, 1500 ft (UMMZ 95478, 95479); 2 mi SW La Resolana, 1100 ft (KU 40125, 40126–40129, 40138, 40139); 1 mi N Barra de Navidad (KU 97242–97244, 97246–97248); 3 mi NW Barra de Navidad, 30 ft (KU 97239–97241); 5 km NNW Barra de Navidad (KU 87455–87465, 87467–87472, 87474–87489); 0.5 mi N Navidad, 25 ft (UMMZ 100654, 100655, 101268–101270); 3 mi E Navidad, 50 ft (UMMZ 100641–100653); Navidad Bay (UMMZ 80912–80914, 80924); 14.5 mi S Pihuamo, 1100 ft (KU 111820–111827); 4 mi NNE Puerto Vallarta, 50 ft (KU 64494–64498); 4 mi SW Puerto Vallarta, 20 ft (KU 111828); 20 km WNW Purificación, 1400 ft (KU 93021, 93652); 30 km N and 10 km E Santiago (KU 87489); El Tabaco, 200 ft (KU 107669–107674); Tenacatita Bay (UMMZ 80897, 80906, 80911). *Michoacán*: 16 mi S Arteaga, 800 ft (KU 40132–40137, 40140); 0.5 mi SE Coalcomán, 3600 ft (UMMZ 100670–100672); near La Huacana (USNM 126497–126501); 1 mi E La Mira, 300 ft (KU 40141–40144); 9 mi S Lombardía, 1500 ft (KU 38652); 7 mi S Tumbiscatio, 2700 ft (KU 40130); Parque Nacional Uruapan (UMMZ 110560, 110561). *Morelos*: Puente de Ixtle (USNM 126943, 127496, 127497). *Nayarit*: Arroyo de Jiguite, Río Santiago, 100 m (USNM 523637, 523638); Aticama, 10 ft (KU 36860–36864); Chacala, 30 m (USNM 509467–509473, 523631–523636); 1 mi S Cuautla, near sea level (USNM 509389–509450, 510551–510560); 1.2 mi S (by road) El Casco, Río Chilte, 480 ft (USNM 511645–511652, 511751, 511752, 511884–511889); El Refilion, 850 m (USNM 509463–509466); 3.5 mi E (by road) El Venado, 100 m (USNM 509455, 510562); Estanzuela, 1380 m (USNM 509474); 1 mi E Ixtlan, 4000 ft (UMMZ 95475); 2 mi E Jalcocotan, 500 m (USNM 523624–523630, 524358, 524359); 1 mi NE Las Piedras, Río Tigrera (USNM 523639, 523640); 5 mi S Las Varas, 150 ft (KU 40124); 8 mi SSW Las Varas (KU 64480–64482); 4 mi NE San Blas, 100 ft (UMMZ 103184–103187); 8.8 mi E San Blas, Paso de Soquilpa, 100 m (USNM 509456–509462, 510563); 10 mi E Ruiz, Platanares (KU 85830, 85831, 85837); 4 mi E Playa Los Corchos (USNM 553966, 554089); San Blas, 75 ft (USNM 89206–89208, 89240); 0.5 E San Blas, 10 ft (KU 36852–36859); 1 mi S San Francisco, 50 ft (KU 64490–64493); 2 mi SW San Juan de Abajo (USNM 512558–512561, 512759, 512760); 2 mi E San Pedro Lagunillas, E side lake, 1300 m (USNM 509474–509493, 510564–510567); 15 km S Santa Cruz, Playa Colorado (USNM 553963–553965, 554088); Santiago, 200 ft (USNM 91403, 91404); Teponahuaxtla (USNM 509451–509454, 510561); 2 mi WNW Valle de Banderas (KU 64483–64489). *Oaxaca*: Cuicatlán, 1800–1900 ft (USNM 69654, 69660); 1 km N Cuicatlán, 560 m (KU 29490–29492); 3 km NNE Cuicatlán, 600 m (KU 29487–29489); 1 km S Cuicatlán, 590 m (KU 29493); 2 km SSW Cuicatlán, 570 m (KU 29494); Huilotepec, 100 ft (USNM 73408, 73726); Llano Grande, 200 ft (USNM 71406, 71407, 71921, 73727, 73730); Plumas, 3000 ft (USNM 71415, 71417, 71418); Puerto Angel, 100–200 ft (USNM 71408–71414, 73745); Tehuantepec (USNM 73407). *Puebla*: Piaxtla, 3900 ft (USNM 70273–70276). *Sinaloa*: 2 mi E Costa Rica, 100 ft (KU 100502–100508); 24 km S Guasave, 20 ft (KU 90316); 3 mi N Higueras, 30 ft (KU 96669–96674); 6 mi NNW Teacpan, Isla Palmito del Verde (KU 98960, 98961); 6 mi W La Concha, 10 ft (KU 98962, 99156); 5 mi NW Mazatlán (KU 85825–85829); Rosario, 100 ft (USNM 91405); 8 km N Villa Unión, 450 ft (KU 96099, 96100); 1 mi N Zaragoza, 30 ft (KU 90314, 90315). Sonora: San José de Guaymas (UCLA 51021, 51026, 51038).

Oryzomys nelsoni Merriam, 1898

Oryzomys nelsoni Merriam, 1898: 15. *Type locality*: Mexico, Nayarit, Tres Marías Islands, María Madre Island, 800 ft; *holotype*: USNM 89200 (skin and skull), an adult male collected 13 May 1897 by E.W. Nelson and E.A. Goldman.

Oryzomys palustris nelsoni, Hershkovitz, 1971: 704 (name combination, listed as valid subspecies).

DISTRIBUTION: Known only from Isla María Madre, the largest of the Tres Marías, Nayarit.

REMARKS: Merriam (1898, 1901) aptly captured the distinguishing characteristics of his new form, in particular its large skull, massive and strongly decurved rostrum, and large, broad incisors (figs. 8, 9). Dimensions

that reflect Merriam's qualitative descriptions, particularly those measured on the rostrum, figure prominently among the several variables that account for isolation of the four specimens of *O. nelsoni* in discriminant-function analyses (table 4). Merriam also mentioned the island form's large body size, long tail, and big hind feet; in relative and absolute size, *nelsoni* possesses the longest tail among the species of the *O. couesi* group in western Mexico (table 2). Examples of *O. albiventer* lack such a robust rostrum and upper incisors as found in *O. nelsoni* but possess heavier molars (table 2). We must accept that the morphology evident in the small museum series of the Tres Marías Oryzomys is typical of the species. Sadly, *O. nelsoni* represents an instance where the investigator's sample statistics and population parameters are one and the same.

SPECIMENS EXAMINED: Mexico, *Nayarit*: Tres Marías Islands, Isla María Madre (USNM 89200–89203).

Oryzomys peninsulae Thomas, 1897

Oryzomys peninsulae Thomas, 1897: 548. *Type locality*: Mexico, Lower California [Baja California Sur], Santa Anita; *holotype*: BMNH 98.3.1.107 (skin and skull), a male collected on 23 May 1896 by Dane Coolidge.

Oryzomys palustris peninsulae, Hershkovitz, 1971: 704 (name combination, listed as valid subspecies).

Oryzomys couesi peninsularis, Alvarez-Castañeda, 1994: 99 (incorrect subsequent spelling, assessment of conservation status).

Oryzomys couesi peninsulae, Alvarez-Castañeda and Cortés-Calva, 1999: 448 (name combination, treated as valid subspecies).

EMENDED DIAGNOSIS: A species of the *O. couesi* group characterized by a combination of moderate size (larger than *O. couesi mexicanus*, smaller than *O. albiventer*) and dorsal pelage of head and forequarters predominantly gray toned. Cranium with deep braincase, zygomatic arches broadly spreading and squarely shaped, and incisive foramina long and exceptionally broad. Upper incisors relatively deep and curvature more nearly orthodont.

DISTRIBUTION: Known only from two localities in southernmost Baja California Sur, Nayarit.

REMARKS: Merriam (1901) and Goldman (1918) were clearly impressed by the differentiating traits of *O. peninsulae*, as emphasized by Thomas (1897), and many of their qualitative characterizations of its distinctly shaped skull contributed to its morphometric separation (e.g., "high braincase," "large and broadly open palatal slits," "rather large molars"). The pelage contrast between the grayish-brown forequarters and fulvous brown hindquarters is still appreciable in the century-old, now slightly faded skins that Nelson and Goldman collected at San José del Cabo and is unmatched for its constancy in other western Mexican *Oryzomys*. The orthodont shape of the upper incisors (fig. 9) impresses us as also diagnostic of the species, but the feature was not mentioned by the aforementioned authors.

The *Oryzomys* population isolated at the southernmost tip of the Baja Peninsula was maintained as a valid species until grandiosely synonymized under *O. palustris* by Hershkovitz (1971). Hall (1981: 610–611) later provided some post hoc rationale for its subspecific rank within *O. palustris* and considered "the degree of difference between *O. peninsulae* and *O. palustris mexicanus* of the eastern coast of the Gulf of California to be less than between some intergrading subspecies of *O. palustris* (e.g., *O. palustris texensis* and *O. p. aquaticus*)." Hall's precept for the synonymy of *peninsulae*, the purported intergradation of *texensis* and *aquaticus*, has proven to be erroneous, the latter forms instead representing nonintrogressing races of the species *O. palustris* and *O. couesi*, respectively (Benson and Gehlbach, 1979; Schmidt and Engstrom, 1994). As we document above, the morphological identity of *O. peninsulae* is sharply and uniquely circumscribed relative to populations of *O. couesi mexicanus* and other *Oryzomys* in western Mexico. Such a "degree of difference" clearly advises specific recognition until controverted by other evidence.

SPECIMENS EXAMINED: Mexico, *Baja California Sur*: Santa Anita (BMNH 98.3.1.107, USNM 93398); San José del Cabo (USNM 146607–146620, 147340).

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APPENDIX 1

Supplementary Specimens Examined

The following specimens were additionally consulted apropos evaluation of taxa in western Mexico, but no decision about their status was reached. The pro forma listing as subspecies of *O. couesi* reflects their current classification (i.e., Hall, 1981), not a taxonomic recommendation.

Oryzomys couesi aztecus: Mexico, *Morelos*, Yautepec, 4100 ft (USNM 51171, 51172, 51173 [holotype], 51174, 51175); 10 mi S Cuernavaca (USNM 20907/36019).

Oryzomys couesi crinitus: Mexico, *Distrito Federal*, Tlalpan, 7600 ft (USNM 50181, 50182 [holotype], 50183).

Oryzomys couesi regillus: Mexico, *Michoacán*, Los Reyes (USNM 125936–125940, 125943, 125944, 125945 [holotype], 125946–125948); 1.5 N Los Reyes, 4400 ft (KU 96101–96103); 1.5 mi S Los Reyes, 4500 ft (KU 96104).

Chapter 4
The Antiquity of *Rhizomys* and Independent Acquisition of Fossorial Traits in Subterranean Muroids

LAWRENCE J. FLYNN[1]

ABSTRACT

In parallel with the growing body of molecular data bearing on the relationships of muroids, particularly subterranean lineages, the relevant fossil record has improved to the point that its data constrain scenarios of evolution about both the timing and mode of evolution of burrowing muroids, especially bamboo rats, blind mole rats, and zokors. Morphologists have considered these groups phylogenetically distinct from each other, but the three lineages appear to be related as a monophyletic Family Spalacidae, sister taxon to all other living muroids, based on both nuclear and mitochondrial genes. Although living genera are fully subterranean, the fossil record shows that the three groups evolved burrowing characteristics independently. Bamboo rats (Rhizomyinae) have the longest fossil record, extending into the Late Oligocene, but do not show fossorial traits until the Late Miocene. Blind mole rats (Spalacinae) have a fossil record nearly that long, and its early members also lack burrowing traits. Zokors (Myospalacinae) show characteristics considered derived relative to other groups, and have a shorter fossil record. The fossil record of the Tribe Rhizomyini, living Asian bamboo rats, extends to about 10 million years ago, with early species distinct at the generic level from living *Rhizomys*. The oldest well-known species assignable to an extant genus is *Rhizomys (Brachyrhizomys) shansius* from the early Pliocene of Yushe Basin, China, north of the geographic range of modern *Rhizomys*. A hypothesis of close relationship of bamboo rats, blind mole rats, and zokors leads to a reevaluation of affinities of certain Asian fossil taxa and reevaluation of polarity of some features, but molecular data are not yet robust enough to clarify interrelationships of the groups. Morphological and fossil data suggest that myospalacines are more closely related to rhizomyines than to spalacines, and that known Early Miocene rhizomyines are close to the stem zokor morphotype.

INTRODUCTION

"The panoply of adaptations necessary for living underground in tubular burrows has dramatically defined the blind mole rat phenotype, which facilitates their diagnosis but obscures phylogenetic connections to other muroid rodents." This wonderful statement from Musser and Carleton (2005) could be applied as readily to bamboo rats as to *Spalax*, the blind mole rat. Truly subterranean small mammals are obliged to spend at least 95% of the time underground. Given this condition, adaptive constraints are focused such that phylogenetically remote taxa converge in body form, limb proportions, and skull structure. Old World burrowers like bamboo rats and blind mole rats look like North American gophers and even superficially like lipotyphlan moles. Nevo (1999) explored this very subject in his book on subterranean mammals. Since phenotypic resemblance of rodent burrowers is not an especially strong argument for close relationship, fossorial lineages have been classified separately, often at the family level. Ironically, recent molecular work suggests that several different burrowers constitute, in fact, a monophyletic group.

My personal fascination with bamboo rats and relatives began with research on the Siwalik fossil record of the Indian subcontinent, which contains the lion's share of what is known of the history of the group. The Late Tertiary basins of China, in which I

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have had the pleasure to work with colleagues in the field, also produce bamboo rats, as well as the endemic fossorial muroids known as zokors. It is the fossil record of China that provides knowledge delimiting the origin of the bamboo rat *Rhizomys,* and includes remains of other enigmatic muroid precursors.

This study begins with description of the oldest fossil skull and postcrania of the genus *Rhizomys*, which derives from Pliocene Epoch rocks of Yushe Basin, Shanxi Province, People's Republic of China, and is housed in the American Museum of Natural History, New York. It demonstrates the generic identity of other less complete remains of bamboo rats from the fossil record of China, and sheds light on the systematics of older bamboo rats. This analysis leads to a discussion of the phylogenetic relationships of bamboo rats and the relevant fossil record, given that recent molecular work argues for strong affiliation with *Spalax* and with the diverse but local zokors of eastern Asia. Previously, most systematists had considered the common origin of bamboo rats, *Spalax*, and zokors to be remote in time and likely not monophyletic. Finally, enigmatic elements in the fossil record of China are placed in the context of the evolutionary history of higher muroids, given a hypothesis of close relationship of these burrowing groups.

MUROID SYSTEMATICS

Musser and Carleton (2005) give a thorough accounting of the history of muroid classification. For the purposes of this paper, it is sufficient to note that the monophyly of Muroidea is not a question, nor is (for the moment) the close relationship of South Asian bamboo rats (*Rhizomys* and *Cannomys*) and African mole rats (*Tachyoryctes*). Relevant to the issues explored herein, however, is the family-level division of Muroidea and implied close relationships within those families.

Subdivisions of Muroidea have been evident for many years, and these are treated extensively by Musser and Carleton (2005). While many authors have preferred to utilize the family-level category to recognize these subdivisions, others, including Carleton and Musser (1984) and McKenna and Bell (1997), have elected to give them lower rank (subfamily), pending more data to clarify interrelationships. Such data are emerging from molecular as well as anatomical studies. These tend to endorse the higher categories that are evidenced by morphology (15 subfamilies according to Carleton and Musser, 1984), and to define clusters of them, which correspond to family-level taxa, fewer in number. Current molecular studies (Steppan et al., 2004; Jansa and Weksler, 2004) are beginning to survey Muroidea broadly, but individual efforts still sometimes miss key taxa. The integrative analysis of Musser and Carleton (2005) draws on molecular and morphological data and recognizes six families within Muroidea: Platacanthomyidae (usually not treated in molecular work), Calomyscidae, Nesomyidae, Cricetidae, Muridae, and Spalacidae. Steppan et al. (2004) and Jansa and Weksler (2004) show Spalacidae to be the sister taxon to all other extant Muroidea.

The family-level taxon Spalacidae has come to be seen as a basal survivor of the fabulous radiation leading to crown-group muroids. Spalacidae would be an ancient branch of living Muroidea. Other more primitive muroids, logically treated as independent families, are all extinct. Hence the Eocene and early Oligocene radiations of muroids should be recognized at the family rank (e.g., Eumyidae, Pseudocricetodontidae, Paracricetodontidae, Eucricetodontidae, Tachyoryctoididae; see Ünay-Bayraktar, 1989), and not lumped in Cricetidae. Coming from the molecular work, however, is the somewhat surprising linkage of *Spalax* and *Rhizomys* + *Cannomys* + *Tachyoryctes* with the fossorial zokor *Myospalax*. Musser and Carleton (2005) illustrate the colorful history of classification of these genera and show that they have been associated in the past, but not usually together to the exclusion of all other muroids. Şen (1977) did suspect that these genera belonged together in Family Spalacidae. This is an exciting and testable hypothesis of relationship that makes review of the fossil record of these groups relevant. I begin with the bamboo rats.

Abbreviations

AMNH	American Museum of Natural History, New York
F:AM	Frick mammal fossil collection of the American Museum of Natural History
Fm.	formation
GSP	Geological Survey of Pakistan
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA
THP	Tianjin Huang Pei, fossil collections of the Tianjin Museum of Natural History, P.R.C.

Comparisons: Among a large suite of specimens in the collections of the Vertebrate Zoology Division of the AMNH and in the Mammal Department of MCZ, useful comparisons were made among *Rhizomys pruinosus pruinosus* (AMNH 113477), *Rhizomys pruinosus senex* (MCZ 35935, 35936), *Rhizomys sinensis vestitutus* (MCZ 7559, 7560), *Rhizomys sinensis wardi* (AMNH 115527, 115528), *Rhizomys sumatrensis* (MCZ 61049), and *Cannomys badius* (AMNH 163644, 163645). The AMNH Division of Paleontology also houses several series of elements attributed to fossil *Rhizomys troglodytes*, for example, AMNH 18407 and 18409. Also examined were *Eospalax fontanierii* (MCZ 19896), "*Myospalax* cf. *cansus*" (AMNH 135358, probably *Eospalax fontanierii*), *Spalax microphthalmus* (AMNH 228), *Spalax ehrenbergi* (MCZ 61376) and *Tachyoryctes* sp. (AMNH 54305, 187461).

SYSTEMATICS

Tribe Rhizomyini Winge, 1887
Genus *Rhizomys* Gray, 1831
Subgenus *Brachyrhizomys* Teilhard de Chardin, 1942

Diagnostic Features: The Tribe Rhizomyini is equivalent to Flynn's (1982, 1990) subfamily Rhizomyinae, diagnosed by derived characters including reduction of the ventral slit of the infraorbital foramen, ridge absent on lower incisor enamel, small posterolingual reentrant on m3, reduced incisive foramina, and a host of fossorial features (chisel incisor, strong coronoid process on deepened mandible, modified humerus with broad epicondyles and strong deltoid crest, broad skull with flaring zygoma and lambdoid crest). The genera *Rhizomys* and *Cannomys* are distinguished from earlier taxa by the apomorphic high, round infraorbital foramen lacking a ventral slit, and the latter is derived in its short M3 and m2, reduced posterolophid on m2, and three crests on M2 and m2. *Rhizomys* has a deep dentary and its masseteric crest terminates below the front of m1 or beyond, without an anterior extension, four-crested M1–2 (strong mesoloph), mesolophid indistinct on m3. The subgenus *Brachyrhizomys* is characterized by features that are likely primitive: lower crowned than living *Rhizomys*, m2 longer than wide until late wear, posterolophid on m3 incompletely isolated, masseteric crest not extending past anterior root of m1, lower diastema not shortened. *Brachyrhizomys* appears to be derived in proodonty, but shares this trait with *Cannomys*.

Rhizomys (Brachyrhizomys) shansius Teilhard de Chardin, 1942

Holotype: IVPP 31.096, right dentary with incisor, m1–3; coronoid process, condyle and angle of the mandible missing.

Referred Material: THP 14.183, right dentary fragment with incisor, m2–3; F:AM 117337, cranium and mandible with complete dentition, atlas + axis, partial rib cage and clavicle fragment, right scapula, left and right humerus and ulna, right distal femur fragment, and tibia diaphysis.

Localities and Age: All specimens from Pliocene deposits of Yushe Basin, Shanxi Province, China. North of the Yellow River, in central Shanxi, this basin is north of the range of *Rhizomys* at present. The holotype is of imprecise provenance; THP 14.183 is from Baihaicun, upper Gaozhuang Fm. or lower Mazegou Fm.; F:AM 117337 is from Zhaozhuang, Mazegou Fm., age about 3.5 million years ago (megaannum, Ma). The age range for known fossils, at most 4.5 – 3 Ma, is quite possibly shorter, ~4–3.3 Ma (time scale of Cande and Kent, 1995).

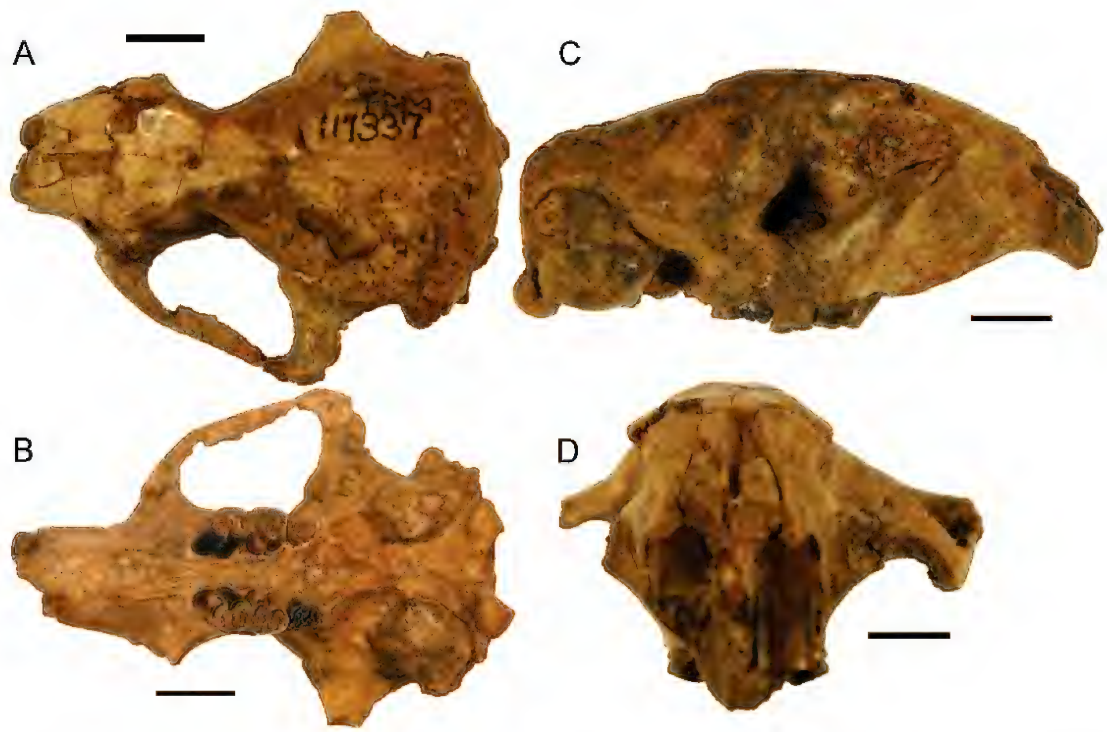

Fig. 1. Cranium of *Rhizomys (Brachyrhizomys) shansius* (F:AM 117337), in dorsal (A), ventral (B), right lateral (C), and anterior (D) views. Scale bars equal 1 cm.

SUPPLEMENTED DIAGNOSIS: *Brachyrhizomys* about the size of smaller individuals of *Rhizomys sinensis* or *R. pruinosus* but with lower crowned molars; skull with proodont incisors, weak lambdoid crest, gently convex occiput nearly vertical and not expanded dorsoventrally; lingual reentrant on M1 short and not convergent with middle buccal reentrant, m2 not wider than long and with persistent anterolingual enamel lake, mandible with diastema not shortened.

DESCRIPTION OF CRANIUM: The skull of *R. shansius* is very much like that of living *Rhizomys*, showing the overprint of adaptations for a fossorial lifestyle. It is compact, stoutly built, with heavy rostrum and broad braincase. There is a narrow interorbital constriction and the occiput supports heavy musculature. The upper diastema rises anteriorly toward the heavy incisors. Tooth rows are set close, with small incisive foramina several mm anterior to them. Significantly different, however, is that the skull, especially the occiput, is lower than that of the high skull of living species; the occiput is clearly wider than high, and less sloping. F:AM 117337 represents a young individual, with last molar still erupting and not yet showing attrition (fig. 1).

The tips of the incisors, nasals, and bits of the premaxillas are missing due to breakage. The incisors were proodont unlike living *Rhizomys*, in which they recurve and are directed ventrally. The incisors appear to be rooted above M1. The snout (fig. 2) is broad posteriorly, and narrows steadily anteriorly; conversely the nasals broaden anteriorly. The narrow posterior limits of the nasals are adjacent to the posterior borders of the premaxillae. Together, these make a jagged intersection with the frontals opposite the posterior rim of the high infraorbital foramen. The dorsal aspect of the infraorbital foramen is ringed by the maxilla. The foramen transmits the deep portion of the masseter, whose scar extends slightly beyond the foramen onto the premaxilla. Anterior to the infraorbital foramen, the premaxilla-

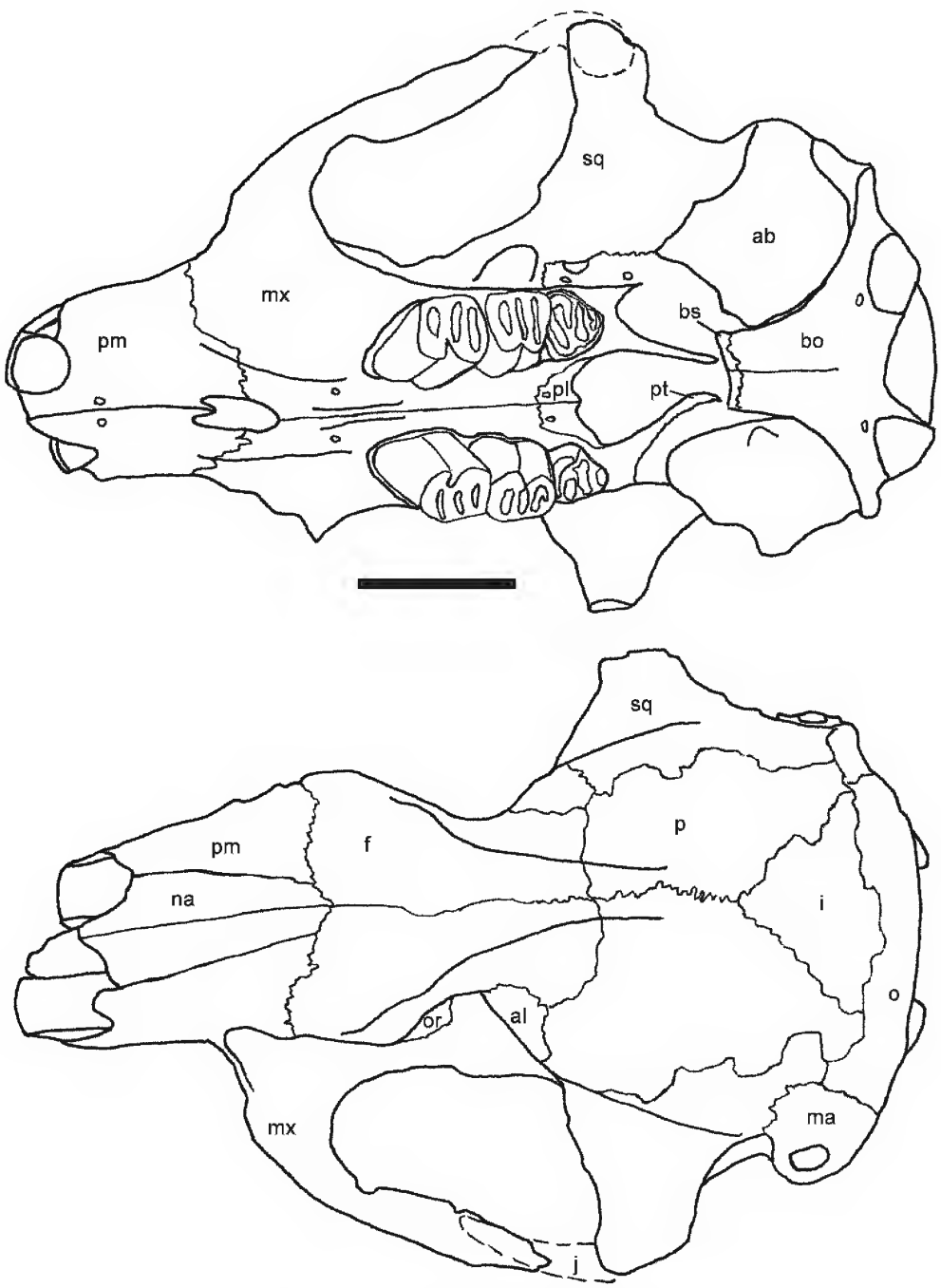

Fig. 2. Line drawing of the skull of *Rhizomys (Brachyrhizomys) shansius* (F:AM 117337), in ventral (above) and dorsal (below) views; 1 cm scale. View is slightly angled to show features of the orbit (deep fissure from ventral view; some of the orbitosphenoid from dorsal view, on the side of the orbit, above the maxilla floor). Abbreviations: **al** (alisphenoid), **ab** (auditory bulla), **bo** (basioccipital), **bs** (basisphenoid), **f** (frontal), **i** (interparietal), **j** (jugal), **ma** (mastoid), **mx** (maxilla), **n** (nasal), **or** (orbitosphenoid), **p** (parietal), **pl** (palatine), **pm** (premaxilla), **pt** (pterygoid), **sq** (squamosal).

maxilla suture drops vertically to intersect the middle of the incisive foramen. The muscle scar of the lateral masseter clearly extends anteriorly on the side of the rostrum beyond this suture. Anterior to the scar is a shallow depression in the premaxillary bone, posterior to the incisors. Because the origin of the lateral masseter is highly developed, it suppresses completely the zygomatic plate, fusing it onto the side of the snout. The infraorbital foramen is high and rounded, fully modern, except that it is proportionately larger than in living species. The anterior root of the zygoma of F:AM 117337 is broken on both sides and the lacrimal bone is not preserved. The lacrimal may contribute to the dorsal aspect of the anterior root of the zygoma in living species but, in any case, does not touch the premaxilla. The heavy left zygomatic arch flares broadly laterally. It was broken during preparation, but the small jugal (fig. 2) was located and replaced. The arch is not as deep dorsoventrally as in living species, and the contribution to it by the jugal bone is smaller.

In dorsal aspect, the interorbital region of the skull is constricted, narrower than the rostrum, rounded around the braincase. Scars for the temporalis muscle begin at the anterior margin of each orbit and converge posteriorly but do not meet. Temporal ridges can be traced caudally to the interparietal and nearly to the occiput before they turn laterally. Both the degree of interorbital constriction and convergence of scars as parasagittal crests are a function of size and individual age. The frontal bones contribute to the anterior portion of the braincase and terminate somewhat posterior to the interorbital constriction. Bones of the cranial vault are thick with sutures reinforced by overlapping laminae of bone, particularly between parietal, interparietal, supraoccipital, and squamosal. Hence, tracing sutures is complicated by minor spalling of laminar bone from the fossil. The parietals roof most of the braincase; the occipital plate does not encroach upon them from behind. The large interparietal is roughly triangular, not subrectangular as in many muroids, and it is large for *Rhizomys*, not overlain posteriorly by the supraoccipital as it is nearly completely so in living species. The occipital is gently convex, not flattened or surmounted by a distinct flange of bone. From the occipital condyles, barely visible in dorsal view, the occiput rises vertically and curves gently rostrally. The dorsal view of the strongly inclined occiput of living *Rhizomys* reveals the condyles prominently.

In posterior view the braincase is much wider than high. Mastoids are prominent. Dorsolateral to them, a wing of the squamosal extends above and medial to the bony auditory tube (broken on the left side). The foramen magnum is large relative to modern *Rhizomys*. Bullae are large and heavy, with a short bony auditory tube present. The bony auditory tube terminates at the level of the posterior root of the zygoma, and does not extend dorsolaterally above the zygoma as in living *Rhizomys*. Paroccipital processes, although broken, probably were not as big as in living species. In ventral view, the basioccipital extends to the mouth of the eustachian canal of the bulla. Wings of the pterygoids are broken, and most of the basisphenoid is missing (fig. 2). The basicranium is telescoped, shortened as in living *Rhizomys*. The telescoping places the bullae adjacent to the pterygoid vacuities. The deep pterygoid vacuities and mesopterygoid fossa accommodate the pterygoid musculature that counters the strong temporalis. The vacuities retain some matrix, obscuring details of the foramen ovale, the middle lacerate foramen, and the alisphenoid canal.

The rostrum and palate are strongly built. Penetrating the bone near the midline and posterior to each incisor are small premaxillary foramina. The rostrum is constricted on each side by the heavy masseteric musculature, which builds a flange of bone along the posterior half of the diastema. These ridges flank short, closely paired incisive foramina, whose posterior ends are 4.4 mm anterior to the alveolus rim for M1. Molar rows are set close and diverge somewhat posteriorly. A ridge down the center of the palate is bounded on each side by a narrow trough. The palatine bone tightly rounds the maxillary alveolus for M3 and contributes to the posterior margin of the hard palate. It terminates with a V-shape at the maxilla, with rostral apex and opposite the boundary between M2 and M3. Posterior palatine

foramina are weakly defined, apparently located at the border with the maxilla. Because the hard palate extends caudally only to the middle of M3 in this young individual, the palatine contribution to the hard palate is minor. The palate ends about 1.7 mm anterior to the posterior rim of the alveolus for M3. The otherwise concave posterior margin of the palate has a midline knob. Laterally, the maxilla extends as a process behind each M3 and is continuous with the pterygoid plate.

One's first impression of the lateral view of F:AM 117337 is that the skull is deep dorsoventrally, a characteristic of *Rhizomys*. The skull roof is arched, highest above the back of the orbit. Deepening is accomplished mainly by dorsoventral expansion of the maxilla, which accommodates the high-crowned molars. The orbit and its structures are extended dorsoventrally, with simultaneously increased basicranial flexion. The expanded maxilla is consistent with the deep rostrum, which rises steeply toward the incisors. The anterior root of the zygoma is anterior to M1. The posterior root begins above the back of M3, is expansive anteroposteriorly, and rises gently rearward. It ends at the posterolateral extent of the temporal ridge, which passes above the auditory tube of the bulla. This tube is more elongate and extends dorsally above the level of the zygoma in living *Rhizomys*. The glenoid fossa is wide and elongate. The heavy posterior root of the zygoma is supported by a large squamosal bone. Relative to the squamosal, the small alisphenoid is squeezed with the maxilla and contributes to the back of the orbit. Posteriorly, the alisphenoid shows a notch, which may represent the anterior opening of the alisphenoid canal. Anterior to this are two foramina, apparently equivalent to the buccinator and masticatory foramina of geomyids (Wahlert, 1985), which also have a deep skull. The floor of the orbit, maxillary bone, is excavated deeply into the skull and includes pits for the sphenoidal (anterior alar) fissure and optic foramen. A small foramen above M1 in the maxilla may be the sphenopalatine. The small orbitosphenoid is located anteriorly at the midlevel of the orbit, and deep within it. The orbitosphenoid and alisphenoid are barely in view from the dorsal aspect (fig. 2). These bones are relatively larger than in living *Rhizomys*, which has a relatively more vertically expanded maxilla. Correlated to the more vertically expanded maxilla, the orbit is less deeply excavated above the molar roots in living species.

MANDIBLE: The unfused mandible has a large, rugose contact surface between dentaries that brings the chisel-shaped incisors close together. Molar occlusal surfaces are tilted inward. The diastema (10.3 mm for the left dentary) is neither as shortened nor as concave dorsally as in living species. Jaw depth is considerable: measured externally, 14 mm below m1, and 13.5 mm below m2. In the young individual represented by F:AM 117337 (fig. 3), m3 is erupting, which makes the measurement of 14.2 mm an underestimate for the length of the tooth row. (The distal wall of m3 slopes ventrally and posteriorly, which makes measurements of the occlusal surface dependent on wear stage). The ventral border of the mature, and larger, THP 14.183 is damaged so that the depth of 15.3 mm below the back of m1 in this specimen is an underestimate for the original; its tooth row length at the alveoli is 14.75 mm. The dentary has a high condyle (10.5 mm above the m2 alveolus in F:AM 117337) and strong coronoid process, perhaps stronger and more vertical than in living species. A prominent coronoid correlates with strong temporalis muscles which stabilize the jaw as the head is lifted during chisel-tooth burrow excavation. The incisor is rooted in a capsule lateral to the condyle. The capsule of this young bamboo rat is smaller and does not extend as far posteriorly as in observed living *Rhizomys*. (*Cannomys* exhibits a condition in which the extended capsule rises above and dominates the adjacent condyle.) The strong upper and lower masseteric crests meet below the front of m1 as a rounded scar without anterior extension. Anterior to it is the mental foramen, above the midline of the dentary, at the back of the diastema. The ascending ramus is broad anteroposteriorly, and rises opposite m2, close to the tooth row and without a defined pocket next to the teeth. The mandibular foramen is above the distal part of m3, not well posterior to it as in living

Fig. 3. Internal (above) and external views of the left dentary, and dorsal view of the right dentary (below) of *Rhizomys (Brachyrhizomys) shansius* (F:AM 117337); scale bars equal 1 cm.

species. The angular process is more caudally extended than in living *Rhizomys*, beyond the limit of the condyle and incisor capsule.

DENTITION: The stout upper incisor is broad mediolaterally (3.45 mm) in relation to its parasagittal length (4.25 mm). Its enamel cap is gently rounded and wraps about three-tenths of the way onto the lateral side of the incisor. There is no major ornamentation—only gentle rugosities on the enamel. The lower incisor (3.91 × 4.35 mm) is heavier, with the enamel cap somewhat less rounded than that of the upper incisor. Enamel wraps just over a quarter of the way onto the lateral side of the incisor. Only minor rugosities ornament the enamel. Although the enamel is considerably darkened, there are mottled traces of original orange pigmentation. The more mature individual THP 14.183 has a larger lower incisor, 4.55 mm wide.

Molar dimensions (length × width) are cited here as maxima, including expanded bases of crowns (not occlusal wear surface; hence, measurements are greater than in table 1). Measurements draw on information from the left and right sides of the skull (differentially preserved and exposed). M1 (6.0 × 4.4 mm) is noticeably longer than wide and moderately high crowned (4 mm crown height visible lingually, less than its length or width). The tooth is higher crowned lingually than buccally and appears to have four roots, one anterolingual root well developed and directed anteriorly for support. The rounded occlusal outline has one lingual reentrant, which extends nearly to the base of the crown. In occlusal view, the reentrant is short and directed anteriorly toward the first of three buccal transverse enamel lakes. Consequently, the tooth exhibits four lophs: anteroloph, protoloph, mesoloph, and combined metaloph-posteroloph. M2 is more squared in its major dimensions (4.3 × 4.25 mm), although it is narrower posteriorly than anteriorly. It has the same four transverse lophs, but the lingual reentrant is directed toward the middle enamel lake, and possibly joined it in early wear. M3 is just erupting, making its measurement (3.8 × 3.6 mm) difficult. It has the same four lophs, although the posteroloph is short due to the rounded nature of the back of the tooth. The lingual reentrant is confluent in early wear with both the anterior and middle buccal enamel lakes.

TABLE 1
Cranial and Dental Measurements (mm)[a] of F:AM 117337, *Rhizomys (Brachyrhizomys) shansius*

Occipitonasal length[b]	55
Zygomatic breadth	46
Interorbital breadth	9.7
Length of rostrum[b]	21
Breadth of rostrum	15.6
Breadth of braincase	24.9
Height of braincase	20.0
Length of diastema	17.9
Length of incisive foramina	4.8
Breadth of incisive foramina	2.5
Length of bony palate	17.6
Breadth across bony palate at M1	3.1
Postpalatal length	20.2
Breadth of mesopterygoid fossa	6.5
Length of bulla	10.7
Crown length of M1-M3[c]	12.2
Breadth of M1, M2, M3[c]	3.9, 3.8, 3.2
Crown length of m1-m3[c]	14.2
Breadth of m1, m2, m3[c]	3.5, 4.4, 4.4

[a] After Musser et al. (2005: fig. 3).
[b] Underestimated due to breakage.
[c] Molar dimensions are at the occlusal surface, and are therefore minimum measurements for these little-worn teeth (the occlusal wear surface is larger in later wear stages).

Lower molars are lower crowned, with less noticeable unilateral height (higher crowned buccally). The first molar (5.2 × 3.95 mm) is well worn although m3 is not fully erupted, and shows primarily five transverse lophs (anterolophid, metalophid, mesolophid, hypolophid, and posterolophid). The mesolophid is a long lingual continuation of the protoconid. A large enamel lake separates the mesolophid from the metalophid and is just closing off from the buccal wall of the tooth at this stage of wear. This lake parallels the major buccal reentrant between protoconid and hypoconid. The posterior enamel lake is small. The m2 is square (4.9 × 4.95 mm; THP 14.183 is somewhat bigger [Flynn, 1993]) and has four major lophs. The short mesolophid joins the anterior loph through the protoconid. Posterolingual to the mesolophid is the hypolophid, which joins the posterolophid lingually. In early wear a small enamel lake in the anterolingual corner of the tooth demar-

Fig. 4. Forelimb of *Rhizomys (Brachyrhizomys) shansius* (F:AM 117337). A, right humerus in medial view; B, left humerus in posterior view; C, lateral view of proximal right ulna; D, medial view of left proximal ulna. Scale bar equals 1 cm.

cates a remnant of the lingual anterolophid. In later wear the mesolophid joins the hypolophid and all lingual reentrants are closed off. The m3 is much like m2 but is longer, especially due to the posterior wall being expanded backward toward its base (7.2 × 5.3 mm). Its small anterolingual lake is persistent and the mesolophid is less prominent, more rapidly merged by wear with the hypoconid. The posterolophid is a simple, prominent, arcuate structure, completely isolated from the rest of the crown by a long reentrant that closes off lingually during moderate wear. The right m3 of F:AM 117337 is somewhat more erupted than the left, shows a bit of wear on its cusp tips although they are below the level of m2, and is partially prepared out of its crypt (allowing crude measurement; crown height about 5.5 mm). It has two lingual reentrants in early wear.

POSTCRANIA: Portions of the axial skeleton of F:AM 117337 are preserved. The broad atlas-axis complex is stoutly built as in living bamboo rats. The proximal two-thirds of a clavicle, 21 mm long, is nearly straight and missing its curved distal end. It is comparable to the stout clavicle of living *Rhizomys*, rather than the more slender clavicle of *Tachyoryctes* or *Cannomys*. The five ribs preserved in near-anatomical position, plus association with other parts of the skeleton and the nearly complete skull, suggest that the specimen was not transported or torn apart by a predator, but perhaps was preserved in its burrow.

The appendicular skeleton includes several parts of each forelimb. The right scapula, with prominent spine but broken acromion and coracoid process, is elongate (24.4 × 11 mm); the supraspinous fossa is narrow, much less expanded than in living species. The ulna (fig. 4) is heavy and anteroposteriorly deep. Broken distally, it exceeds 31.5 mm in length. The olecranon process is prominent, the length from the proximal surface of the trochlear notch to the tip being 9.3 mm. There is a heavy coronoid process and prominent supinator crest running distally from it.

The heavy humerus (fig. 4) has fused, or nearly fused epiphyses. With a length of 34.1 mm, its head is large (maximum dimension and its perpendicular are 10.5 × 9.1 mm). The distal end of the humerus is wide, the epicondylar width being 11.6 mm. The

TABLE 2
Comparative Forelimb Measurements[a] (mm) and Ratios of F:AM 117337, *Rhizomys (Brachyrhizomys) shansius*, and Other Burrowing Muroids

	HL	HW	HW/L	HD	HD/L	UL	OL	OL/UL
Brachyrhizomys shansius (F:AM 117337)	34.1	11.6	0.34	19.0	0.56	>31.5	9.3	<0.30
Rhizomys pruinosus senex (MCZ 35935)	43.0	14.5	0.34	26.1	0.61	48.4	13.7	0.28
R. pruinosus pruinosus (AMNH 113477)	47.2	14.1	0.30	26.1	0.55	55.5	13.5	0.24
Cannomys badius (MCZ 3617)	25.4	7.1	0.28	15.4	0.61	28.2	7.2	0.25
Tachyoryctes ibeanus (MCZ 8134)	25.6	8.0	0.31	14.1	0.55	30.3	6.5	0.21
Tachyoryctes sp. (AMNH 54305)	24.0	6.9	0.29	13.3	0.55	30.3	6.2	0.20
Tachyoryctes sp. (AMNH 187461)	27.0	7.8	0.29	16.0	0.59	35.0	6.7	0.19
Spalax microphthalmus (AMNH 228)	27.0	9.5	0.35	15.8	0.59	33.0	11.3	0.34
Spalax ehrenbergi (MCZ 61376)	18.0	5.8	0.32	12.2	0.68	24.8	8.8	0.35
Eospalax fontanierii (MCZ 19896)	32.0	14.9	0.47	21.2	0.66	43.2	18.0	0.42
Eospalax fontanierii (AMNH 135358)	31.0	15.1	0.49	19.3	0.62	—	—	—

[a] Measurement abbreviations: HL, humerus length; HW humerus width at the epicondyles; HD, distal extent of the deltoid crest of the humerus (measured from the proximal surface of the head of the humerus); UL, ulna length, OL, olecranon length (measured from the proximal surface of the trochlear notch).

prominent deltoid crest is long, ending about 19 mm from the proximal end of the humerus—over half the length of the bone (56%), similar to other *Rhizomys* (table 2). For example, the larger humerus of AMNH 113477 is 47.2 mm long with deltoid crest length of 26.1 mm, 55% its length; its epicondylar width is 14.1 mm, proportionally somewhat less than F:AM 117337. The humerus of *R. troglodytes* AMNH 18407, nearly twice as long as that of *R. shansius*, has a deltoid crest ratio of 63%.

The hind limb is represented by a right distal femur fragment with total condyle width of 11.1 mm. An associated right tibia is missing its epiphyses. The tibia diaphysis is 34 mm long and relatively slender. The scar for the distal portion of the fibula begins 9 mm from the distal end of the diaphysis. Other elements include a proximal phalanx 8.5 mm long.

The forelimb of F:AM 117337 is clearly modified for burrowing, the ulna having a large olecranon process and strong supinator crest, and the slightly twisted humerus having a heavy deltoid crest and wide epicondyles. Epicondyle width, deltoid crest development, and prominence of the olceranon process are developed as in the living rhizomyines *Rhizomys, Cannomys,* and *Tachyoryctes* (table 2). *Spalax* is similar, although its olecranon process is relatively longer. All of these observations appear to be independent of absolute size, as judged from total humerus length, and the features are consistent with burrowing, particularly for rodents that do not rely solely on the forelimbs, but are primarily chisel-tooth diggers. However, the humerus and ulna of zokors, which depend mainly on the forelimb for digging, are strikingly modified. Zokor humeri have prominent deltoid crests that project distinctly from the shaft, and exceedingly broad epicondyles; a tranverse axis through them is angled with respect to the head of the shaft. Humerus width through the epicondyles is nearly half the total length. The olecranon process is long, 42% of ulna length in MCZ 19896, and with a massive proximal tubercle located medially. The forelimbs of zokors show strong adaptations for burrowing, since at least the Late Miocene.

DISCUSSION: Teilhard de Chardin (1942) based his taxon *Brachyrhizomys shansius* on several mandibular fragments from Yushe Basin. Scholars at the Institute of Vertebrate Paleontology and Paleoanthropology determined that the Tianjin collection dentary 31.096 is the type specimen. Its provenance is "Pre-Villafranchian Pliocene beds of Yushe" (Teilhard de Chardin, 1942). Of all known specimens, only F:AM 117337 and a few collected in recent years have good stratigraphic provenance. All are mid-Pliocene in age. Teilhard de Chardin (1942) noted the long diastema and corresponding proodonty

of the incisors, although he determined this without the benefit of a skull to observe! He was also impressed by the lower crown height, hence the name *Brachyrhizomys*. In reality, *Brachyrhizomys* specimens including F:AM 117337 are high crowned, although not hypsodont and not as high crowned as living *Rhizomys*. This feature plus those noted above distinguish *Brachyrhizomys* from living species, but they are largely (if not completely) primitive conditions for *Rhizomys*. F:AM 117337 shows, on the other hand, that *Brachyrhizomys shansius* shares many important derived features with living *Rhizomys*. Fundamental is the infraorbital foramen confined to a high position and without ventral slit—it is sealed ventrally by anterior expansion of the deep masseter. *Brachyrhizomys* shares a high skull profile with *Rhizomys* and other features of the basicranium and palate, plus traits related to burrowing.

Because it is closely related to living *Rhizomys* species, but distinct, *Brachyrhizomys shansius* is treated appropriately as a subgenus within *Rhizomys*. Living forms are all relatively close, distinguished by shared advanced features, and I classify them as *Rhizomys (Rhizomys)*. Features distinguishing *Rhizomys (Rhizomys)* are correlated with the more elevated cranium, which yields dorsoventrally extended orbital structures and a high occiput. The occiput is further exaggerated as a large flat surface area for attachment of musculature used in burrowing.

Among the dozen or so named forms of extant *Rhizomys* (mostly subspecies), systematists consistently recognize three species, *R. pruinosus*, *R. sinensis*, and the larger *R. sumatrensis*. Wang (2003) adds *R. wardi* at the species level. Dental morphology perhaps distinguishes some of the subspecies, for example, the large M3 of *Rhizomys sinensis vestitutus*. *R. shansius* is about the size of small individuals of *R. pruinosus* or *R. sinensis*, but its features do not argue for special affinity with any living species (its M3 size is moderate, judgment made difficult by incomplete eruption). Some authors have placed the large species *R. sumatrensis* in its own subgenus *Nyctocleptes*, but Musser and Carleton (2005) do not follow this; distinctions of this species are largely allometric.

There are also named forms of *Rhizomys* from the Pleistocene fossil record of China. All of these are clearly modern in grade, some assignable to living species, and all can be classified as *Rhizomys (Rhizomys)*. *Rhizomys troglodytes* is like living *R. sinensis* in size, and was compared with the latter by Matthew and Granger (1923). *R. ultimus* Young and Liu (1950) was synonymized with *R. sinensis* by Zheng (1993). Zheng (1993, 2004) conserved *R. troglodytes* and added the small form *Rhizomys brachyrhizomysoides* as extinct bamboo rats from eastern Sichuan Province and from Hubei Province. Wei et al. (2004) named *Rhizomys fanchangensis* from Anhui Province, assigning it to the living genus based on similar dentition, which is consistent with incisor orthodonty of the fossil material. This oldest described *Rhizomys* (*Rhizomys*) dates to the early Matuyama magnetic chron, greater than 2 Ma.

Brachyrhizomys shansius is known for remains from Yushe Basin. The species name is applied by Zheng (1993) to fossils said to be from the Zhoukoudian Cap Travertine, but I have not seen these specimens. The Yushe fossils are all Pliocene in age. Flynn (1993) added a new, small species to the Yushe fossil record, *Rhizomys (Brachyrhizomys) shajius*, based on a single dentary from Late Miocene deposits. Like *B. shansius*, this species is primitive in its unshortened diastema, moderate crown height, m2 longer than wide, and termination of the masseteric crest under m1 (not more anteriorly). A recalibrated paleomagnetic age for *Brachyrhizomys shajius* is 5.9 Ma. This species is significantly older than *B. shansius* and much smaller (estimated m1–m3 length, 9.3 mm).

Flynn (1982) applied the name *Brachyrhizomys* to large, fossorial bamboo rats from the Siwalik deposits of the Indian subcontinent. The several Siwalik species share a number of features with *B. shansius* (and living *Rhizomys*), and are distinct from other large fossil bamboo rats, such as *Rhizomyides sivalensis*. However, the Late Miocene Rhizomyini, as exemplified by GSP 8362 (Flynn, 1982, pl. 2), do not show the derived closure of the ventral slit of the infraorbital foramen of *B. shansius*. Also, GSP 8362 is a low skull and not as broad and wedge shaped as

AMNH 117337. These Siwalik bamboo rats and Miocene age representatives from southern China cannot be maintained in the taxon *Brachyrhizomys*, and require a new generic level name.

Miorhizomys, new genus

TYPE SPECIES: *Miorhizomys nagrii* (Hinton, 1933); illustrated in Flynn (1982).

INCLUDED SPECIES: *Miorhizomys blacki* (Flynn, 1982), *Miorhizomys choristos* (Flynn, 1982), *Miorhizomys harii* (Prasad, 1968), *Miorhizomys micrus* (Flynn, 1982), *Miorhizomys nagrii* (Hinton, 1933), *Miorhizomys pilgrimi* (Hinton, 1933), *Miorhizomys tetracharax* (Flynn, 1982).

DIAGNOSIS: (after Flynn, 1982, characteristics for "*Brachyrhizomys,*" which were drawn mainly from these fossil species) Rhizomyini with moderately deep dentaries and a masseteric crest lacking a strong anterior extension, lower crest not inflated; lower incisor usually with flattened enamel and no median ridge; molars relatively small and of moderate crown height, with unilateral hypsodonty; M1 rounded anteriorly, without anterolingual flexus; m3 with small posterolingual enamel lake and often a deep buccal reentrant; incomplete closure of ventral slit of the infraorbital foramen; pronounced fossorial adaptations. In addition, *Miorhizomys* shows low elevation of the skull, m2 with three roots and strong mesolophid, and a longitudinal connection (mure) on m2 and m3.

AGE AND GEOGRAPHIC RANGE: Late Miocene of southern Asia, from Pakistan to Yunnan.

ETYMOLOGY: *Mio-* (prefix derived from the epoch during which this bamboo rat genus thrived) plus *rhizomys* ("root rat").

DISCUSSION: *Miorhizomys* is a rhizomyine genus showing fossorial adaptations, but is not as derived as either *Rhizomys* or *Cannomys*. The Siwalik fossil genus *Rhizomyides* Bohlin, 1946, is a large tachyoryctine, and more distantly related. *Anepsirhizomys* Flynn, 1982, is another large genus of unclear affinity to which Flynn (1990) transferred the species *A. pinjoricus* (Hinton, 1933). *Miorhizomys* shows remarkable diversity shortly after its appearance in the fossil record of the Indian subcontinent. Oldest records date to about 9.6 Ma, with age of actual appearance likely to be no greater than 9.9 Ma (Barry et al., 2002). By about 9 Ma, four species were present. The genus continued to be diverse through at least 8 Ma, probably later, and is well represented in the Late Miocene of northern India. Flynn (1985) pointed out that high diversity and cladogenesis are not unexpected for a fossorial rodent. Flynn and Qi (1982) noted broad distribution of rhizomyines across southern Asia into Southeast Asia, and cited some of the same species at Lufeng, Yunnan Province, as in the Siwaliks. Recent reexamination of original, large samples of the Lufeng material (personal observation) confirms that the Lufeng species are very close to, but not all identical with the Siwalik species. They are certainly congeneric.

Tribe Rhizomyini, all members of which show fossorial adaptations, appeared during Late Miocene time around 10 Ma. The early genus *Miorhizomys* ranged throughout southern Asia, from Pakistan to Yunnan, and was successful as measured by high species richness. The species of *Miorhizomys* are the ecological precursors to modern *Rhizomys*, which appeared about 6 Ma in China and became established during the Pliocene. Given late fossil occurrences for a group considered to be of remote common ancestry with other muroids (Steppan et al., 2004; Jansa and Weksler, 2004), it is important to review the record of older rats potentially related to them.

KEY CONSTRAINTS FROM THE FOSSIL RECORD

As so eloquently stated by Musser and Carleton (2005, above) the fossorial habits of *Rhizomys*, *Spalax,* and *Myospalax* have led to skeletal modifications that overprint the features primitively characterizing each clade. The similar adaptations across the genera, but lack of these in early members of each clade, makes diagnosis of rhizomyines, spalacines, and myospalacines difficult. Review of the fossils attributed to each group places in context not only the antiquity of each, but allows a judgment of the likelihood of their interrelationships and focuses on any direct

evidence for burrowing adaptations in these lineages. The analysis below suggests that each group acquired full fossoriality independently.

Subfamily Rhizomyinae

Flynn (1982) revised knowledge of the evolution of rhizomyines, benefiting from a greatly expanded fossil record, primarily from the Siwaliks of Pakistan. His diagnosis for the higher taxon (his Family Rhizomyidae) including extant *Rhizomys*, *Cannomys,* and *Tachyoryctes* noted the muroid condition of three cheek teeth, the advanced muroid condition of myomorphy, proodonty (some forms orthodont), lophodonty (transverse crests as high as cusps), and differential hypsodonty, with upper molars markedly higher crowned internally than externally. There is also a strong molar wear gradient in all rhizomyines: first molars are always much more worn than posterior molars. Musser and Carleton (2005) cautiously regard *Tachyoryctes* as potentially independent of *Rhizomys* and *Cannomys*. However, some South Asian fossils, such as *Eicooryctes* argue that tachyoryctines were widespread in the Late Miocene (Flynn, 1982), and not an independent African group.

Morphology: An important feature in tracing the evolution of muroids is the character state of the anterior part of the zygomatic arch, and the muscle scar of the masseter. In hystricomorphs, the deep part of the masseter penetrates the enlarged infraorbital foramen and originates on the snout; the lateral part of the masseter is confined to the ventral border of the arch. Muroids show progressive myomorphy in which the lateral masseter extends anteriorly on an expanded zygomatic plate. This plate rises anteriorly, constricting the infraorbital foramen ventrally, but leaving a slit behind. Advanced myomorphs extend the origin of the lateral masseter anteriorly by adding a projecting flange onto the plate. Lindsay (1977) hypothesized gradational transformation of hystricomorphy to myomorphy in muroids, early taxa (Oligocene) being hystricomorphous (barely any expansion of the lateral masseter origination) or showing low inclination of the zygomatic plate.

Flynn et al. (1985) found rhizomyines to cluster among derived muroids in their myomorphy—they were not a part of the early radiation of muroids that were typically hystricomorphous. The myomorphous condition of Rhizomyinae is modified further with respect to many living muroids by a degree of closure of the ventral part of the keyhole-shaped infraorbital foramen. In later rhizomyini, the ventral notch of the keyhole opening is totally eliminated, leaving only a dorsal hole in *Rhizomys* and *Cannomys* (autapomorphy for this pair of genera). Less modified rhizomyines are represented by *Tachyoryctes* and 9 Ma *Miorhizomys* and *Kanisamys*, which show abbreviated ventral notches. These taxa can be reinterpreted as showing an early stage in the transformation of myomorphy from hystricomorphy, while *Rhizomys* and *Cannomys* show secondarily reduced myomorphy. They are a product of muroid evolution at a time when the myomorphous condition had not reached full development of an expanded, high-angle zygomatic plate with deep ventral slit.

Rhizomyinae are derived with respect to many Paleogene muroids in loss of the archaic posterior connection of the protoconid and metaconid on m1. The posterior connection runs directly from the protoconid, or from its posterior arm, transversely to the metaconid. Early rhizomyines may display an ephemeral posterior connection, but also lack an anterior connection. A firm connection of the anterior arm of the protoconid to the metaconid developed in later *Kanisamys* (Flynn, 1982) in parallel to that trend in other Miocene muroids. This observation agrees with the early stage of myomorphy in plotting rhizomyines among derived, but not modern muroids.

Rhizomyines possess persistent longitudinal ornamentation on the enamel of the lower incisor. As in many late Oligocene to Early Miocene muroids, a double ridge occurs on the incisor in early species. By the Late Miocene this is a single ridge, which persists throughout Tribe Tachyoryctini. This condition is transformed again in Tribe Rhizomyini in which ridges are totally absent.

These features imply origin of rhizomyines (and spalacids in general) from Late Oligocene muroids that already displayed a degree of myomorphy, suppression of the archaic posterior connection between metaconid and protoconid of m1, and the then widespread occurrence of persistent ridges along the midline of the enamel of the lower incisor. Muridae and Cricetidae are Miocene derivatives of a more advanced stock of muroids.

Fossil Record: The Siwalik Group deposits, primarily in Pakistan, contain a relatively complete series of bamboo rat fossils, filling the gap between standard muroids and living rhizomyines. Small Miocene species of the genera *Prokanisamys* and *Kanisamys* are abundantly preserved in successive horizons spanning > 20 to 8 Ma (de Bruijn et al., 1981; Flynn, 1986; Wessels and de Bruijn, 2001). Postcrania show that these species were not obligate fossorial rodents. There are some digging modifications in the humerus of *Kanisamys sivalensis* (about 9 Ma), but they are not striking. In contrast, beginning after 10 Ma, other large-body species do show fossorial adaptations in the skull and forelimb. These have been gathered under the names *Rhizomyides* and "*Brachyrhizomys*" (now *Miorhizomys*). Flynn (1985) saw the Late Miocene species-rich pattern of occurrence of large-bodied *Miorhizomys* as consistent with fossorial lifestyle (underground habitus promoting isolation and splitting). Apparently, bamboo rats were initially terrestrial scratch diggers; commitment to subterranean life came later and independently in different groups.

The fossil record of rhizomyines is substantially older than the first evidence for fossoriality, but just how old is this lineage? The emerging pre-Siwalik fossil record shows greater antiquity for the group than previously in evidence. Lindsay (1996) described the oldest rodent attributable at present to the bamboo rat lineage. Under the name *Eumyarion kowalskii* (in earlier works he mentioned this as an unnamed species of *Eucricetodon*), he showed the beginnings of the lophodont rhizomyine dentition, modified from the basic cricetid plan, and preserving, variably, the archaic posterior connection between protoconid and metaconid on the m1. Its elevated crown height is barely advanced over that of typical muroids. The studied sample is from the Zinda Pir Dome, western Pakistan, locality Z113. Isolated incisors from Z113 show a double ridge on the enamel. The age of this site is demonstrably younger than the classic Bugti Oligocene sites of Paali Nala (Welcomme et al., 1999) and Z108 and Y417 (Flynn and Cheema, 1994), and older than Early Miocene sites in the area. Analysis of the magnetic polarity stratigraphy of the Zinda Pir Dome (Lindsay et al., 2005) allows two reasonable correlations to the geomagnetic polarity time scale, which place the site at about 24 or 27 Ma (near the Oligocene-Miocene boundary or during the Late Oligocene). Thus, the oldest rhizomyines appear to antedate other spalacid muroids.

Subfamily Spalacinae

In summarizing the spalacine fossil record, Ünay (1999) noted that rhizomyines, spalacines and other lineages of burrowers appear to be distinctive throughout most of their histories, at least in dental characteristics (fig. 5), although all converge in adaptations to fossorial lifestyle. Potapova and Vorontsov (2004) agreed and noted convergence in auditory structures correlated with subterranean life. Paleontologists, therefore, have considered the spalacines to be distinct at the family level from other muroid groups. Three morphological features have tended to support the apparently remote ancestry of *Spalax*: (1) The expanded infraorbital foramen is round (but not reduced and dorsal in position) and lacks an inclined myomorphous zygomatic plate; the lateral masseter origin is clearly defined, but restricted to the ventral border of the zygoma, close to the condition seen in hystricomorphs. (2) The lower first molar lacks the anteriorly placed connection between the protoconid and metaconid (the posterior metalophid is generally lost as well). (3) The lower incisor shows very weak if any longitudinal ornamentation, unlike most Late Oligocene–Miocene muroids. Given the data then at hand, Flynn et al. (1985) concluded that spalacines were of ancient origin from hystricomorphous muroids that lacked advanced molar structure and incisor ridges. It

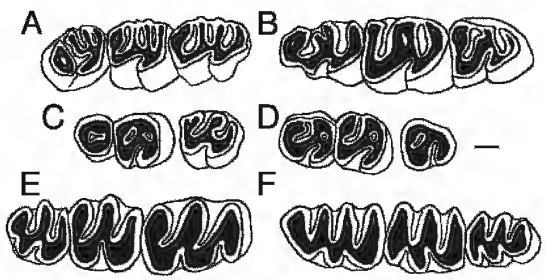

Fig. 5. Comparisons of upper and lower molars of a generalized rhizomyine (A, B), spalacine (C, D), and myospalacine (E, F). Molar rows are composites of fossils, except E and F, which are associated. Seen left to right, A (right M3 to M1) and B (left m1 to m3) are based on *Kanisamys sivalensis* from Flynn (1982). C (worn right M3–M2 and separate M1) and D (left m1 and m2 and worn m3) are based on *Pliospalax macoveii* from Şen (1977). E (right M3 to M1) and F (left m1 to m3) are based on *Mesosiphneus praetingi* from Teilhard de Chardin (1942). Scale is 1 mm.

appeared that rhizomyines were more derived in these features.

The spalacines have a modern distribution from the Mediterranean area throughout eastern Europe to western Asia, with extinct species of *Spalax* and *Pliospalax* recorded widely in Eurasia, but not the Far East. The fossil record is Early Miocene and younger. The Oligocene *Rhizospalax* is a beaver (Hugueney and Mein, 1993). The late Early Miocene *Heramys* Klein Hofmeijer and de Bruijn (1985) shows several spalacine features (lophodonty, high molar crowns, loss of metalophid on m1), but retains a large m3. Ünay (1996) added to the fossil record the more primitive, lower-crowned genus *Debruijnia*, which shows a variable metalophid connection on m1. The age of the earliest species of this genus is ca. 20 Ma. Neither *Heramys* nor *Debruijnia* indicate fossoriality, but postcrania are unknown.

Sarica and Şen (2003) added key fossil remains from the early Late Miocene Sinap Formation of Turkey. These revealed important anatomical details of spalacines in the 11 to 9 Ma age range. Sarica and Şen (2003) named *Sinapospalax* for an array of species that share robust dentaries, lophodont molars, and incisors bearing multiple longitudinal ridges. *Sinapospalax* showed that ridges were indeed present on early spalacine incisors. Further, the robust dentaries suggest that these muroids were proodont burrowers.

Generally considered separate but closely related are the extinct anomalomyines, characterized primarily by *Anomalomys* and *Prospalax* (Fejfar, 1972). These have a similar age range as spalacines, but are confined to Europe. Bolliger (1999) reviewed the group and noted the presumed fossorial habitus of later species. Following de Bruijn and Saraç (1991), he further drew comparison to the Early Miocene muroid *Eumyarion*, based on molar similarities and the double ridge of enamel along the length of the lower incisor. *Eumyarion* is known from the Early Miocene of Turkey (Ünay-Bayraktar, 1989), as well as Pakistan (above), older than *Anomalomys* or *Debruijnia*. If anomalomyines and spalacines are closely related, Late Oligocene origin of this group would be probable.

Despite the projected Oligocene origin for spalacines and their apparently primitive morphology, the oldest clear spalacine fossils are younger than the earliest rhizomyines. Still, given that spalacines and *Anomalomys* may share common ancestry with a morphotype resembling *Eumyarion*, one can hypothesize close relationship to the earliest rhizomyines, a hypothesis consistent with molecular data. The features of early spalacines are now better known, and may be reinterpreted as similar to those of early rhizomyines, not more primitive. Early members of both groups show enamel ornamentation and similar m1 morphology. The undeveloped zygomatic plate of *Spalax* and *Pliospalax*, possibly a reversal, does differ from the stronger plate of early rhizomyines.

Skull and postcranial remains, rare before the Late Miocene, show that *Pliospalax* was an active burrower (Şen, 1977). The robust, proodont dentary of *Sinapospalax* also suggests burrowing. However, there is no evidence for fossoriality in early spalacines, and the conservative dentitions of *Heramys* and *Debruijnia* suggest that these were not obligate burrowers. Present evidence indicates independent acquisition by the early

Late Miocene of the subterranean lifestyle in rhizomyines and spalacines.

Subfamily Myospalacinae

Whereas spalacines and anomalomyines are European-Mediterranean and western Asian rodents, and rhizomyines are primarily South Asian–East African, myospalacines (zokors) are common eastern Asian burrowers, typical of much of northern China and Mongolia and ranging into southern Siberia, the Altai Mountains, and eastern Kazakhstan. Living species, up to about 250 grams in body mass, are highly derived subterranean small mammals that dig with their forelimbs (Nevo, 1999). They have adopted, therefore, a different strategy than rhizomyines and spalacines, which utilize the incisors extensively in burrowing.

Living myospalacines comprise at least seven species (Musser and Carleton, 2005), which can be assigned to two genera, *Myospalax* and *Eospalax*. The fossil record of myospalacines in China is extraordinarily rich, and appears to show geographic differences, with different species as contemporaries in eastern and central China. Most researchers acknowledge broad morphological diversity among the array of fossil zokor species. Zheng (1997) recently rearticulated his rationale for diagnoses of generic and higher level groupings (here, tribes). In Prosiphneini Leroy, 1940, he groups *Prosiphneus* Teilhard, 1926, *Myotalpavus* Miller, 1927, *Pliosiphneus* Zheng, 1994, *Eospalax* Allen, 1938, *Allosiphneus* Kretzoi, 1961; in Mesosiphneini Zheng, 1994, he places *Chardina* Zheng, 1994, *Mesosiphneus* Kretzoi, 1961, *Yangia* Zheng, 1997 (= *Youngia* Zheng, 1994); in Myospalacini Lilljeborg, 1866, are *Episiphneus* Kretzoi, 1961, and *Myospalax*, Laxmann, 1769. This diversity reflects a high degree of cladogenesis, likely promoted by isolating mechanisms correlated with solitary lifestyle and small home ranges.

Structural characteristics of myospalacines include a zygoma interpreted as myomorphous, although the infraorbital foramen is not strongly keyhole shaped and the zygomatic plate is not expansive or greatly inclined, a forelimb highly derived for burrowing, and superficially prismatic molars. It is clear that their prismatic (*omega form* is a better term used by Carleton and Musser, 1984) condition is derived convergently with respect to the much more complex molar shapes of arvicolines. The lower first molar presents an anterior connection between the anterior arm of the protoconid and the metaconid, which appears to be the derived muroid condition. It could have been constructed independently, much the same way as it developed in rhizomyines. Also like earlier rhizomyines and various muroids, the lower incisor is always characterized by a single longitudinal ridge. These morphological features suggest that myospalacines evolved from later muroids more derived than the ancestral stock for spalacines.

The fossil record demonstrates rapid diversification of zokors, with most of the splitting during the past 10 million years. The oldest species attributed to early *Prosiphneus* date to over 11 Ma according to Zheng et al. (2004). As research has developed in China, scientists have traced the origin of the myospalacines to the Middle Miocene muroids *Plesiodipus* Young, 1927, or *Gobicricetodon* Qiu, 1996, both in excess of 12 Ma (see Wang et al., 2003). It seems logical to transfer these genera to the Myospalacinae. However, *Plesiodipus* is comparable to generalized cricetids, the family in which Qiu (1996) classifies it, and *Gobicricetodon* is low crowned, although robust. Probably these earliest myospalacines were not truly fossorial. More likely, myospalacines acquired fossoriality independently about 11 Ma, an independence consistent with characteristic forelimb-digging in contrast to chisel-tooth digging in rhizomyines and spalacines.

Conclusions based on morphology and the fossil record are: (1) Zokors show derived features (myomorphy, anterior metaconid-protoconid connection, incisor ridge) suggesting derivation from Miocene muroids. (2) Zokors evolved forelimb burrowing independently about the beginning of the Late Miocene. (3) Zokor origin appears to be Middle Miocene; the common ancestor of *Myospalax* and *Spalax* must be much older than the known range of myospalacines, and more basal among murids. The Middle Miocene zokor origin conflicts with a Plio-

cene estimate by Michaux and Catzeflis (2000). Norris et al. (2004) discounted a Pliocene split based on molecular grounds, and found that mitochondrial genes place *Myospalax* basal to *Spalax* and *Rhizomys*. Jansa and Weksler (2004) reanalyzed the von Willebrand Factor (vWF) gene results of Michaux and Catzeflis (2000) and also placed *Myospalax* outside the other spalacids. However, a maximum-likelihood analysis of the first exon of the IRBP gene placed *Myospalax* somewhat closer to rhizomyines (Jansa and Weksler, 2004) and showed that the geometry of the three taxa is not yet understood robustly. A monophyletic relationship with *Spalax* and *Rhizomys,* in which *Myospalax* is the most basal form, is unexpected from morphology and the fossil record. This relationship disrupts character distributions and calls for a zokor lineage back to the end of the Oligocene, which is nowhere in evidence. As noted below, nesting of zokors within Miocene rhizomyines seems more conceivable.

Other Chinese Fossil Muroids

The enigmatic *Pararhizomys* and *Tachyoryctoides* have been implicated in the evolution of bamboo rats. *Pararhizomys hipparionum* is a Late Miocene species from Mongolia and North China that presents rhizomyine-like features with some exceptions. Dentition is lophodont and rather high crowned, and skull material shows modified myomorphy (reduced ventral slit of the infraorbital foramen), as in late Neogene rhizomyines. Unlike rhizomyines the molar wear gradient is even (not markedly stronger anteriorly). Unlike most rhizomyines but like spalacines, third molars are reduced, and m1 lacks a metalophid. The lower second molar has two buccal reentrants, the anterior one bounded by a strong buccal extension of the anterolophid. This buccal anterolophid is normally suppressed in rhizomyines, but present in early species, and conserved in myospalacines. Unlike *Rhizomys* but like *Tachyoryctes*, the near-flat incisor of *Pararhizomys* shows a single longitudinal ridge. Myospalacines conserve the ridge as well. The skull of *Pararhizomys* is strongly built, but not wedge shaped like a committed fossorial rodent. It is rather low and elongate (Kowalski, 1968), comparable perhaps to that of a small *Marmota*.

Pararhizomys is known from several Late Miocene sites of North China (Zhang et al., 2005). The genus may also be recorded from the Late Miocene of Tibet. *Brachyrhizomys hehoensis* Zheng, 1980, from Biru, Bulong Basin, is unusual for rhizomyines (small m3, even molar wear) and may be a member of the genus *Pararhizomys* (Jacobs et al., 1985).

Zhang et al. (2005) evaluated proposed *Pararhizomys* relationships to rhizomyines, spalacines, myospalacines, and tachyoryctoidines, and found two most probable scenarios: *Pararhizomys* is a primitive rhizomyine or a derivative of independent early muroid origin. I cannot improve on this suggestion at present other than to emphasize that if *Pararhizomys* is a rhizomyine, it is not closely related to living bamboo rats. The odd m2 reentrant and retention of the incisor ridge would be primitive structures modified in Rhizomyini. The elevated molar crown height reminiscent of spalacines and Tribe Tachyoryctini likely evolved independently. In building a hypothesis of sister-taxon status for spalacines and rhizomyines, it is conceivable to include *Pararhizomys* as a member of that clade, outside Tribe Rhizomyini. Further, if myospalacines are indeed part of the spalacine-rhizomyine radiation, then *Pararhizomys* could root close to the origin of Myospalacinae, possibly among Middle Miocene rhizomyines.

Oligocene to Early Miocene *Tachyoryctoides* shows no special features to align it with either rhizomyines or spalacines. Its characteristics illustrate primitive muroid features. The cheek teeth are rather low crowned. The crests are not transformed as sweeping lophs, but rather, in early wear, as thin interconnections with deep reentrants. The primitive muroid buccal arm of the anterolophid is well developed on m2 and m3. Reminiscent of the spalacine condition of m1, there is no direct connection of the protoconid and metaconid. *Tachyoryctoides* has almost no mesolophid on lower molars; upper molars have a very short mesoloph, but are four-crested due to a long posteroloph emanating from the hypocone. In the absence of cranial material, the masseteric

condition may be inferred from the mandible. The masseteric crest is quite heavy, flaring laterally and terminating opposite m2, although a weak portion of the scar extends below m1. Probably a heavy lateral masseter originated from the bottom of the zygoma. The lower incisor is heavy and distinctly flattened, lacking a ridge, but with low thickenings of enamel along both the medial and lateral borders. The chisel-like incisor is consistent with digging, but until postcrania or skull material are described, fossorial adaptation for *Tachyoryctoides* is poorly supported.

Tachyoryctoides is distributed throughout northern China and Mongolia, and westward to the Aral Sea region, as a common component of Oligocene and Early Miocene assemblages. It is thus a contemporary of the basal rhizomyine *Eumyarion kowalskii*. The differences in the structures of these taxa show that *Tachyoryctoides* is not a rhizomyine. Flynn (1982) agreed with Fejfar (1972) that the genus could be a primitive spalacine, but that idea comes from the similar m1 structure. Otherwise, there are no special features shared with *Heramys* or with *Anomalomys*. Consequently, *Tachyoryctoides* is not readily associated with either rhizomyines or spalacines, and at present its sister status with rhizomyines + spalacines cannot be defended.

DISCUSSION

The Tribe Rhizomyini arose late in bamboo rat evolution, after 10 Ma, and all fossil members show burrowing adaptations. Likely their success reflects radiation into the subterranean niche, and exploitation of available underground resources. Early species lack some of the advanced fossorial traits of extant taxa, and cranial fossils demonstrate that they are not assignable to *Rhizomys* or *Cannomys*. The new generic name, *Miorhizomys,* is created for the Late Miocene radiation of subterranean bamboo rats. It is characterized among other features by retaining an abbreviated ventral portion of the myomorphous infraorbital foramen. *Miorhizomys* was distributed across southern Asia from Pakistan in the west to Yunnan Province in the east. The oldest known *Rhizomys* is from the Late Miocene of northern China, 5.9 Ma, but the oldest well-represented species is *Rhizomys (Brachyrhizomys) shansius* from the early Pliocene of Yushe Basin, Shanxi Province. Osteological material consisting of the skull and anterior parts of the axial skeleton, parts of both forelimbs, and a partial hindlimb shows that by the Pliocene, Chinese bamboo rats were fully modern with advanced burrowing adaptations and derived skull structure, especially the modified, high and round, infraorbital foramen of living species.

The pattern of evolution of burrowing rodents appears to be linked to opportunities to exploit available subterranean ecological space (Nevo, 1999; Cook et al., 2000). Controlling factors would include availability of underground food sources and quality of the soil (including rockiness and moisture). One hypothesis sees radiation of subterranean rodents and emergence of hominids as phenomena connected to the evolution by plants of underground nutrient-storing organs, which would be highly desirable food sources (Laden and Wrangham, 2005). The data to test these ideas come from the fossil record, and for rodents include constraining the timing of acquisition of fossorial traits across lineages. How muroids, in particular, acquired subterranean lifestyles is relevant to testing whether burrowing evolved in this group due to availability of a new food source. If bamboo rats, the blind mole rat (*Spalax*), and zokors are confamilial (Steppan et al., 2004; Jansa and Weksler, 2004), then early acquisition of burrowing traits might be proposed as a synapomorphy uniting them (Norris et al., 2004). It turns out that the pattern of evolution of fossoriality in these muroids shows late and independent commitment to subterranean lifestyles. Fossorial features cannot be used to define Spalacidae cladistically, and probably evolved in the early Late Miocene to exploit new food sources.

Rhizomyines have the longest known fossil record of the three subfamilies. Early forms (Late Oligocene and younger) clearly were not obligate subterranean dwellers. Full fossoriality appears only after 10 Ma. The known time depth of spalacines rivals that of rhizomyines, but osteological evidence for

burrowing is rather young. Dental remains indicate lack of features, like high-crowned, lophodont teeth, that are correlated with burrowing. In contrast, the known time range of zokors is hardly half of the other groups, and morphological features suggest that zokors represent a later radiation. Middle Miocene zokor species show no evidence of fossoriality, but fossil representatives of the radiation after 11 Ma include humeri modified for burrowing. Independent acquisition of full burrowing adaptations in each muroid group appears to be the pattern. Independence is underscored by the forelimb burrowing in zokors that contrasts with the chisel-tooth digging of bamboo rats and blind mole rats.

Despite independent and divergent means of solving the problems of subterranean life, the three groups may have evolved from generalized muroid scratch-diggers that lived in burrows, but were not fully subterranean. The fossil record should be consistent with such a hypothesis, and is relevant for constraining the timescale of evolution. The oldest known spalacids are Late Oligocene, 27 Ma at most. Under this scenario, the spalacid group would have originated in the Late Oligocene and the three lineages would have adopted fully subterranean lifestyles later, probably not before the Late Miocene.

Given that molecular and morphological data place Spalacidae as a basal group among all other (studied) living muroids, origination dates for all other muroid groups would be younger than 27 Ma, which is a maximum estimate for the earliest known spalacid fossil. A younger, Miocene, age for the appearance of other extant muroid families would be expected.

Herein, morphological features used to evaluate relationships have been reinterpreted given the molecular hypothesis of spalacid monophyly. Impressed by differences between spalacines and rhizomyines, Flynn (1982) had considered the former as primitive and to have originated significantly earlier. The zygoma of *Spalax* was interpreted as hystricomorphous, instead of myomorphous with a weakly inclined plate, the smooth incisor enamel was taken as primitive (not as secondary loss of ornamentation), and molar lophs were considered underived (which they are, as are early rhizomyines, relative to most Miocene taxa).

The constructive challenge of new molecular data leads to reappraisal of character states, which properly entails a survey of the extant muroids (since spalacids are basal), plus well-known key fossil taxa (appendix 1). This survey makes use of the mammal collections of the AMNH and MCZ and of available casts of fossil material. There are far too few character states for the 400 living and fossil muroid genera to allow informative phylogenetic analysis using parsimony, but a tree can be generated as a testable hypothesis (fig. 6) using the relationships of living families established on molecular grounds. Injecting fossil taxa into a tree generated by molecular data is provocative in stimulating a hard look at both character definition and polarity on the one hand, and assumptions about molecular evolution on the other. It is hoped that this hypothesis will stimulate a deep and extended search for characters and a new survey of fossil taxa to generate a more rigorous test.

A tree (fig. 6) showing both living and fossil groups allows reanalysis of character distributions. Salient morphological features that can be observed on the tree include: early muroids are hystricomorphous and later genera show modifications of the zygoma, including progressive inclination and expansion of the plate, the posterior connection of m1 is lost, followed by construction of an anterior connection, and incisor ornamentation is a conservative feature that appears among muroids and then is lost. Other features of the dentition are overlain on the tree (fig. 6) with polarity proposed by outgroup comparison.

Character states for stem spalacids may be reinterpreted as follows: (1) The common ancestor had a zygomatic structure advanced over hystricomorphy but incompletely myomorphous, with moderately inclined zygomatic plate not defining a narrow ventral slit and without an anteriorly expanded flange. (2) The first lower molar had lost its posterior connection but variably showed a remnant of a protoconid-metaconid bridge, and lacked a new anterior connection. (3) The lower incisor was ornamented with a pair of

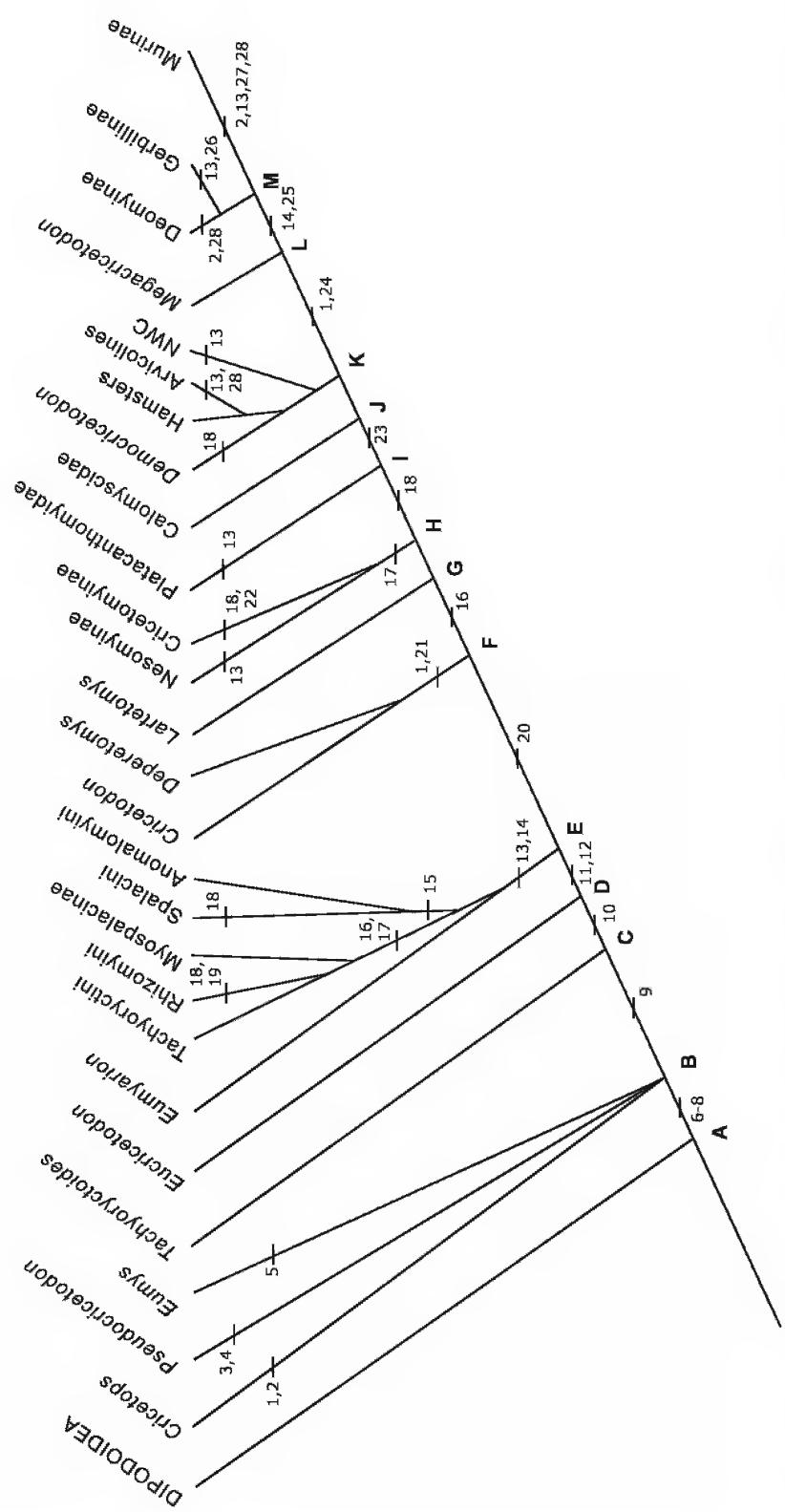

Fig. 6. Phylogenetic tree depicting arrangement of major living groups of muroids plus key fossil taxa, with Dipodoidea as outgroup. This hypothesis depends on molecular data to arrange the living groups, and uses a set of characters (appendix 1) with proposed polarities to plot the fossil taxa. Homoplasy is clear and there are far too few characters to run an analysis based on parsimony. Note that under this analysis, certain higher taxa in occasional usage such as Cricetodontidae need significant revision or abandonment.

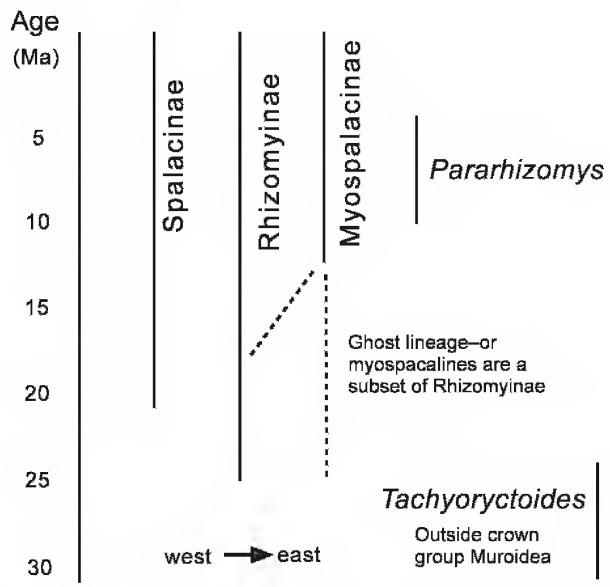

Fig. 7. Known age ranges of the three spalacid subfamilies and key taxa discussed in the text. These are arranged, west to east, according to geographic range, although rhizomyines extend as far eastward (but to the south) as do myospalacines. Rhizomyinae have the longest known age range. Known myospalacines, beginning with *Gobicricetodon* at about 13 Ma, have a much shorter age range. This implies two hypotheses (dashed): either the group has a long ghost lineage, or it is in fact a derivative (infrafamily) of Subfamily Rhizomyinae. *Pararhizomys* may also be a member of Rhizomyinae. *Tachyoryctoides*, on the other hand, does not show spalacid synapomorphies and is excluded from Spalacidae.

parallel, raised ridges. Later derived transformations included: (1) elimination of the ventral portion of the infraorbital foramen in later rhizomyines, but restriction of the lateral masseter to the zygomatic arch in spalacines, (2) neomorphic establishment of a connection to the metaconid from the anterior arm of the protoconid in rhizomyines and myospalacines, (3) loss of incisor ridges in later spalacines and successive reduction from two to one to none in rhizomyines, a single ridge conserved in myospalacines.

Myospalacines present features derived with respect to stem spalacids, but consistent with earlier rhizomyines. Muroids more derived than spalacids adopt the advanced anterior connection for m1, lose incisor ridges, and progressively build the modern myomorphous zygoma, including a strongly inclined plate, usually with ventral slit, and often expanded anteriorly with a flange to offer greater origination area for the lateral masseter muscle.

The scenario favored here, given molecular constraints that unite these muroids, is that Spalacidae originated during the late Oligocene, and that Spalacinae and Rhizomyinae are sister taxa that split shortly thereafter (fig. 7). Myospalacinae are more derived and a younger group that would be closer to Rhizomyinae than to Spalacinae. Character distributions are most consistent when myospalacines are considered as derived from Early Miocene rhizomyines. This also reduces the apparently long ghost lineage leading to the first zokor fossils (fig. 7). If this hypothesis is maintained, myospalacines may be reconsidered as a taxon of lower rank within Subfamily Rhizomyinae.

Among enigmatic Asian fossil taxa, some may have been part of the spalacid radiation. Possibly *Pararhizomys* from the late Neogene of Mongolia and northern China is an early rhizomyine-zokor derivative. The archaic Asian *Tachyoryctoides*, however, is distinguished as a primitive muroid excluded from Spalacidae.

CONCLUSION

There is irony in the maturing analysis of basal muroid groups. It is those scientists

studying morphology (and paleontologists necessarily emphasize morphology) who conclude independence of bamboo rats, blind mole rats, and zokors, and suspect that similar degrees of fossoriality and the attendant "panoply of adaptations . . . obscure[s] phylogenetic connections" (after Musser and Carleton, 2005). It is molecular biologists (e.g., Jansa and Weksler, 2004; Norris et al., 2004) who indicate that these lineages are actually closely related, and imply shared predisposition to subterranean life. While not falsified by morphology or the fossil record, this scenario is constrained by the distribution of features and by paleontology. There is no evidence for subterranean lifestyle among early members of any of the groups. Each group developed fossoriality in Middle to Late Miocene and younger members, and burrowing features cannot be used to diagnose Spalacidae cladistically. Of the three groups, zokors present more derived conditions in dentition and skull morphology, and they have the shortest fossil record.

The origin and radiation of *Rhizomys* is a late event in muroid evolution. Fossil representatives close to extant species occur throughout much of China and Southeast Asia during the Pleistocene. Early Pliocene fossils show the derived conditions of living *Rhizomys*, especially the ventrally constricted infraorbital foramen and features of the skull and humerus associated with a subterranean mode of life. Skull features are, however, generally less derived than those of living species. The best represented Pliocene bamboo rat is from strata of Yushe Basin, Shanxi Province, dating to around 3.5 Ma, and is distinguished at the subgenus level as *Rhizomys (Brachyrhizomys) shansius*. The oldest known *Rhizomys* at 5.9 Ma is also from Yushe. Earlier during the Late Miocene, more primitive bamboo rats were distributed across southern Asia, from Pakistan to Yunnan. Diverse species, many gathered under the new name *Miorhizomys,* show fossorial characteristics but are less derived than *Rhizomys*. Still older nonfossorial Rhizomyinae can be traced to the late Oligocene cricetid-like species *Eumyarion kowalskii*.

Molecular data strongly argue for closer relationships of Spalacinae, Rhizomyinae, and Myospalacinae with each other than with any other living muroids, but do not yet demonstrate which two of the three subfamilies are most closely related. Morphology and the fossil record appear to argue against myospalacines being more basal than the others. Zokors share more features with Rhizomyinae than with Spalacinae, but are not part of the modern bamboo rat tribe. It is reasonable to consider zokors and fossil *Pararhizomys* as derivatives of early rhizomyine evolution.

It is important to continue testing the hypothesis of monophyly of *Spalax* + *Rhizomys* + *Myospalax*. More genetic evidence is likely to clarify the interrelationships of the three taxa from a molecular point of view. This will help to focus reanalysis of polarity of morphological features and the pattern of evolution of these structures. Clearly the demands of a fossorial lifestyle encourage morphological convergence. Could the evolution of some molecules be channeled by selection? Studying more genes is welcome, but also expanding the data set to capture other distantly related burrowing muroids might help. *Ellobius* is perhaps the most fossorial of several burrowing arvicolines, and based on morphology, would not group with spalacids. Inclusion of this and other taxa in the muroid genetic sampling serves as a test of observed relationships. It is the integration of molecular, morphological, and natural history data, and continual testing of hypotheses of relationship and pattern of evolution that promise to advance understanding of the course of muroid evolution. This is what Guy Musser knows so well.

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APPENDIX 1

Notes for Cladistic Relationships of Selected Muroidea[2]

NODES:

A. As outgroup to Muroidea, Dipodoidea illustrate character polarity (P4 present, hystricomorphy, poorly developed anterior cusps on first molars). These two superfamilies constitute a well-defended infraorder Myodonta Schaub (see, e.g., Vianey-Liaud, 1985).

B. This polytomy does not differentiate between *Cricetops*, *Pseudocricetodon*, or the American taxon *Eumys*. All three lack derived character states in m1 morphology, zygomasseteric structure, and incisor ornamentation, which are tracked in more derived taxa. *Cricetops* appears to conserve the primitive zygomasseteric condition of hystricomorphy; *Pseudocricetodon* has a weakly inclined masseteric plate (Lindsay, 1977), and *Eumys-Leidymys* show a plate inclined toward a very high infraorbital foramen (the height seems to be an autapomorphy, Hartenberger, 1967).

C. *Tachyoryctoides* shows low zygomatic plate inclination, hence weak myomorphy. Its flat incisor has no median ridges. These features are taken to indicate a more basal position than *Eucricetodon*, but it is also conceivable that these character states are overprinted by modifications and the position could be reversed with that of *Eucricetodon*.

D. *Eucricetodon* presents moderate zygomatic plate inclination, and is thus modernized; this is also the first taxon to show the widespread double ridges on lower incisors.

E. *Eumyarion* plots as the immediate sister taxon to all living spalacids; here I extend the strong case of de Bruijin and Saraç (1991) for affinity of *Eumyarion* with anomalomyines, to affinity with all spalacids. Within Spalacidae, anomalomyines are close to spalacines, and myospalacines share features with rhizomyines.

F. *Cricetodon* and the closely allied *Deperetomys* show a more modern zygoma than do *Eucricetodon* or *Eumyarion*: more inclined plate with a ventral trough or slit. This condition is observed in nesomyids. The double ridge on the incisor is retained.

G. *Lartetomys* is placed here to signify stable presence of the new anterior connection of m1; that is, a crest running from the anterior arm of the protoconid to the metaconid.

H. Nesomyids present the modern m1, but variably developed myomorphy. Here the primitive character states for the group are interpreted to be m1 anterior connection present, one incisor ridge retained, moderate myomorpy. The Malagasy nesomyines retain the incisor ridge, but develop myomorphy variably, some genera showing a strongly inclined plate; continental cricetomyines lost the incisor ridge (a very weak ridge is sometimes observed), but do not develop myomorphy (some are nearly "hystricomorphous").

I. Based on AMNH specimens of *Typhlomys cinereus*, the inclined zygomatic plate is not developed in keyhole fashion; the ventral slit is not compressed and there is no flange of the plate expanded anteriorly. Neither fossil nor living genera are known to show incisor enamel ornamentation (Kalthoff, 2000; personal commun.). Tentatively placed in a position more derived than nesomyids, but lower than calomyscids, platacanthomyids have not yet been evalu-

[2] Letters refer to comments for nodes and chosen taxa, and numerals represent key characters plotted on the cladogram. This tree presents an explicit hypothesis for testing; it is not an attempt at full phylogenetic analysis of the superfamily (see fig. 6).

ated with other muroids on the basis of molecular data; they could lie outside nesomyids. The group displays extreme lophodonty.

J. Calomyscidae is represented by *Calomyscus*, which is of modern cricetid-murid grade. It is modern in zygomasseteric structure (strongly inclined plate, with ventral slit), in m1 morphology (anterior protoconid connection to metaconid; metaconid relatively anterior in position), and in suppression of the incisor enamel ornamentation (there remains a faint striation on *C. baluchi*). Wessels (1999) lists Late Miocene records for the genus, based primarily on small third molars and lack of mesoloph/-id, and argues for gerbil relationship. However, the simple anterocone/-id and strong longitudinal crest of these fossils are not consistent with gerbil relationship. Placement of Calomyscidae here follows Jansa et al. (2006) and Steppan et al (2004).

K. Fossil *Democricetodon* represents stem cricetids. Its myomorphy is advanced, with the ventral slit of the infraorbital foramen pinched in keyhole fashion, and the M1 has an expanded anterocone. Relationships of groups of cricetids are informed by both the fossil record and molecular data. NWC (New World cricetids) have a late Early Miocene record, younger than the oldest *Democricetodon* (Jacobs and Flynn, 2005).

L. *Megacricetodon* is a derived muroid showing a double anterocone on M1, an elongated anteroconid on m1, and reduced mesoloph/-ids. Third molars are generally reduced. These features place *Megacricetodon* close to murid ancestry (Flynn et al., 1985), and as outgroup to murines plus deomyines, could reasonably be seen as a basal murid, not assigned to a subfamily. This hypothesis seemed weak in 1985, but Lazzari and Aguilar (2007) have documented high variability in large samples of Middle Miocene (ca. 16 Ma) *Megacricetodon*, including occasional presence of accessory cusps in the positions of the classic murid morphology (anterostyle on M1 lingual to double anterocone, enterostyle adjacent to protocone), which makes this genus a reasonable murid outgroup. *Potwarmus* Lindsay (1988) shows M1 morphology near that of murids with stable presence of the enterostyle, but m1 is conservative; the genus would fall near node M on the cladogram.

M. Jaeger (1977) laid the morphological groundwork for realization that gerbils had something to do with murid origination. Inclusion of extinct myocricetodontines among gerbils provided a deep fossil record to envision close relationship. Wessels (1996) documented the richness of myocricetodontine diversity, including taxa with accessory cusps; this Early and Middle Miocene radiation is consistent with closeness of true gerbils and the small Deomyinae group, including very murinelike genera. Sister status of Deomyinae and Gerbillinae was found by Steppan et al. (2004) and Jansa et al. (2006). Sarich (1985) had discovered 20 years earlier that the deomyine *Acomys* plotted outside murines. Myocricetodontines and gerbils present a characteristic pattern of alternating cusps in m1. Special features of murines (and some gerbils and deomyines) include reduction of longitudinal crests and realignment of the power stroke in chewing (Lazzari et al., 2008). Distinctive murine molar morphology with stable accessory cusp pattern and propalinal mastication either appeared independently among certain deomyines, or this complex suite of features was simplified secondarily in gerbils (and some deomyines).

CHARACTERS:

1. Double anterocone on M1. Some muroids have transversely twinned anterocone cusps. This derived condition is found in isolated genera, plus a radiation of advanced muroids, including Muridae.

2. Double anteroconid on m1. This feature does not occur without presence of character 1. However, not all muroids with a double anterocone have a double anteroconid.

3. Pinnate incisor ornamentation. Autapomorphy for *Pseudocricetodon* among genera surveyed here.

4. Low inclination of zygomatic plate. Lindsay (1977) cites a measure of 10 degrees, barely advanced over hystricomorphy.

5. Zygomatic plate inclined to high infraorbital foramen. Hartenberger (1967) shows that the precociously inclined zygomatic plate of Oligocene North American genera reflects the high position of the infraorbital foramen.

6. Central anterocone on M1. All muroids share a distinct anterocone that is near the midline of the tooth (not in extreme buccal position).

7. Expanded anteroconid on m1. Dipodoids have a small anteroconid (if any).

8. P4 absent. Correlated with characters 6 and 7, muroids lack the small, peglike P4 of dipodoids.

9. Moderate zygomatic plate inclination. Lindsay (1977) measures 29° and higher for *Eucricetodon* and other Miocene genera.

10. Double longitudinal ridge on the enamel of the lower incisor (present through node F).

11. Anterocone on M1 expanded in transverse anteroloph.

12. Posterior connection on m1 weak or absent. The widespread primitive condition of a crest joining the metaconid directly to the protoconid or its posterior arm is reduced and lost in Early Miocene lineages. Later changes include anterior shift of the metaconid cusp and construction of a new connection from the anterior arm of the protoconid to the metaconid. This new connection is not the same as linkage to the metaconid from the lingual side of the anteroconid.

13. Lophodonty. This condition unites spalacids, but arose independently in other groups, including arvicolines, gerbils, platacanthomyids, some murines, and some New World cricetids; it is widespread but not universal in nesomyines, and occurs in cricetomyines.

14. Reduced anterior cingulum on M2 and M3. The primitive cingulum is suppressed in many genera. Its suppression unites spalacids and is usual in later muroids.

15. Infraorbital foramen expanded and origin of lateral masseter confined to ventral border of zygomatic arch. This condition appears to be a reversal from the trend of developing full myomorphy, and characterizes Spalacinae (unknown in Anomalomyini) and several other living genera, e.g., *Deomys*.

16. Anterior connection on m1 from the anterior arm of the protoconid to the metaconid. This condition characterizes derived muroids after Node F, and appears to have been developed independently in Rhizomyinae + Myospalacinae.

17. Single ridge on lower incisor enamel. Reduction from two ridges to one is observed within the genus *Kanisamys* (Flynn, 1982) and is evident in Nesomyinae.

18. Absence of ridges on lower incisor. This trait evolved in parallel in Spalacinae, Rhizomyini, and Cricetomyinae. It would characterize all higher muroids, except that some south Asian *Democricetodon* show the double ridge.

19. Infraorbital foramen transformed as a high, rounded opening in the anterior root of the zygoma.

20. Zygomatic plate large and inclined. *Cricetodon* and later muroids are clearly more derived in myomorphy (relative size, anterior expansion, inclination) than any spalacid. Although zygomatic plate size is difficult to evaluate given allometric scaling (*Cricetodon* is larger than *Eucricetodon*) its prominent zygomatic plate resembles that of nesomyines.

21. Thick, wrinkled enamel on molars links the clade of cricetodontine genera (Rummel, 1999).

22. Reduced inclination of the zygomatic plate. Molecular data link nesomyines and cricetomyines. Whereas nesomyines generally retain the zygomatic plate, it is reduced in most cricetomyines, greatly so in some, such as *Steatomys*.

23. Full myomorphy. Full myomorphy means presence of a keyhole infraobital foramen, the upper part of which transmits the medial masseter muscle onto the side of the snout, and the lower part of which is compressed by anterior expansion of the lateral masseter onto an expanded zygomatic plate; this plate is often built anteriorly as a flange of bone lateral to the foramen. This condition is plotted for muroids based on widespread distribution. It is important to note the high frequency of variant zygomatic structures, some of which represent character reversals. The feature is not distributed consistently even within small, well-defined clades. Within cricetines (hamsters) for example, *Cricetus* shows rather typical myomorphy, but *Cricetulus* lacks the zygomatic flange.

24. Prominent, elongated anteroconid on m1. Whereas the anterocone of M1 is expanded and prominent along much of this tree, the anteroconid is often small, and its longitudinal extent is not great. All murids have a prominent anteroconid and most have twinned cusps (character 2).

25. Frequent accessory lingual cusps on upper molars, and buccal shelf with cusps on lower molars. This appears occasionally in *Megacricetodon* and *Sindemys* as a variable trait.

26. Anterocone on M1 and accessory cusps simplified. In gerbils the M1 is simplified by variable reduction of the doubled anterocone and loss of lingual cusps.

27. Murine plan for first molars: M1 with lingual cusps stable in position (anterostyle linked with double anterocone, enterostyle always adjacent to protocone) and m1 with X-shaped double anteroconid-protoconid-metaconid). These features are present in some deomyines (e.g., *Acomys*).

28. Anteroposterior power stroke in chewing. Most rodents, including many muroids, have an oblique component to mastication, and chew preferentially with alternate jaws. A few lineages of rodents develop fully propalinal mastication, nearly perfectly anteroposterior in direction. This feature characterizes true murines, and deomyines for the most part, but gerbils preserve an oblique chewing component (Lazarri et al., 2008). Although propalinal mastication arises in parallel among distantly related rodents, the character serves as a derived condition for murids.